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ORIGINAL PAPER

Run for your life, but bite for your rights? How interactions between natural and sexual selection shape functional morphology across habitats

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Abstract

A central issue in evolutionary biology is how morphology, performance, and habitat use coevolve. If morphological variation is tightly associated with habitat use, then differences in morphology should affect fitness through their effect on performance within specific habitats. In this study, we investigate how evolutionary forces mold morphological traits and performance differently given the surrounding environment, at the intraspecific level. For this purpose, we selected populations of the lizard *Podarcis bocagei* from two different habitat types, agricultural walls and dunes, which we expected to reflect saxicolous vs ground-dwelling habits. In the laboratory, we recorded morphological traits as well as performance traits by measuring sprint speed, climbing capacity, maneuverability, and bite force. Our results revealed fast-evolving ecomorphological variation among populations of *P. bocagei*, where a direct association existed between head morphology and bite performance. However, we could not establish links between limb morphology and locomotor performance at the individual level. Lizards from walls were better climbers than those from dunes, suggesting a very fast evolutionary response. Interestingly, a significant interaction between habitat and sex was detected in climbing performance. In addition, lizards from dunes bit harder than those from walls, although sexual differentiation was definitely the main factor driving variation in head functional morphology. Taking into account all the results, we found a complex interaction between natural and sexual selection on whole-organism performance, which are, in some cases, reflected in morphological variation.

Keywords Morphological traits · Habitat use · Performance · Natural selection · Sexual selection

Introduction

A central theme in evolutionary biology is to understand how phenotypic variation evolves and how the phenotype is related with the environment. Morphological traits are a substantial part of the phenotype: they are the structural components with which organisms interact with their environment. As such, they are involved in very different and crucial ecological and social functions, and they are subject to strong selective influences. Selection can be described as the relationship between variation in phenotypic traits and variation in fitness across individuals (Kingsolver and Huey 2003). Differences in an organism's functional morphology should result in differences in performance that directly affect fitness in a given environment (Arnold 1983; Emerson and Arnold 1989; Irschick 2002), yielding links between morphology, performance, and fitness that have been studied under the framework of the ecomorphological paradigm (Arnold 1983).

Selection pressures act on individuals, maximizing their chances for survival and reproduction, which is why the approach described by Arnold (1983) was initially put forward at the intraspecific level, and in particular highlighting

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the relevance of "*the analysis of adaptation within populations of conspecifics*" (Arnold 1983: 348). However, similar approaches have been used extensively to study macroevolutionary associations between morphology, performance, and ecology across species. For instance, *Anolis* lizards are one of the most remarkable examples of an adaptive radiation where sympatric species have repeatedly evolved divergent morphologies, performance, and behaviors as means of exploiting different microhabitats and enhancing niche segregation (Losos and Sinervo 1989). This and other textbook ecomorphological examples have attracted attention in part due to the remarkable morphological diversity they encompass, which makes patterns of variation easier to detect. Indeed, because the magnitude of variation is big, it is generally easier to identify differences among groups and associate them to hypothesized explanatory factors at higher taxonomic levels than within species (Losos and Miles 1994; Kaliontzopoulou et al. 2010a). However, when examining species that encompass a wide evolutionary array, in many occasions, the detected phenotypic patterns and associations across traits can be the result of adaptation or exaptation (sensu Gould and Vrba 1982), evolutionary signal (Blomberg and Garland 2002), or phenotypic plasticity (Losos et al. 2000) potentially making the interpretation of the results difficult. Hence, studies at the intraspecific level are relevant for detecting microevolutionary mechanisms and linking them to adaptive pressures that lead to phenotypic differentiation (Irschick et al. 2005a).

To optimize whole-organism performance, natural and sexual selection mold morphological traits that are involved in ecological functions (e.g., feeding, escape from predators, habitat and refuge use, competition with heterospecifics) and social interactions (e.g., antagonistic behavior, territory and mate acquisition, mating), respectively. Natural selection may influence performance and morphology to enhance the survivorship of the individuals when performing different tasks (Husak and Fox 2006). For instance, when escaping from predators, a fast locomotor performance will be the best strategy to avoid predation, but the probability of survival can be further augmented through morphological adaptations that facilitate the use of specific refuges (Goodman 2009). On the other side, sexual selection may influence performance and morphology to provide individuals with an advantage in mating through intrasexual competition and mate choice (Husak and Fox 2008). For instance, increased locomotor and bite performance enhance the capacity of males for defending territories and increase their mating possibilities (Husak et al. 2006; Husak and Fox 2008). These processes occur simultaneously, and they can be parallel, when both natural and sexual selection act on performance and/or morphological traits in the same way to enhance fitness, or opposite, if ecological and social functions impose conflicting performance demands (Husak et al. 2006; Husak and Fox 2008). The balance between natural and sexual selection is complex, but it can be generally inferred when observing variation in the degree of sexual dimorphism depending on the ecological context (Butler et al. 2000; Butler and Losos 2002; Husak and Fox 2008; Kaliontzopoulou et al. 2010a, 2012).

Lizards provide excellent models for studies of functional morphology because of their wide range of morphologies and performance skills, and of their presence in a variety of habitats (Arnold 1998; Garland and Losos 1994; Irschick and Garland, 2001; Irschick 2002). Further, they are usually sexually dimorphic in body size and shape, where males are frequently larger, with larger heads and longer limbs, whereas females tend to have longer inter-limb length (Kaliontzopoulou et al. 2012, 2013; Gomes et al. 2016; Irschick and Higham 2016). These differences probably result from sexual and fecundity selection, and they occur in morphological traits with a high functional relevance (e.g., Kaliontzopoulou et al. 2010b, 2012, 2013). This provides the opportunity of combining morphological, functional, and ecological data to investigate how natural selection—e.g., with respect to habitat variation—and sexual selection are integrated to shape functional and morphological diversity, and to decipher the evolutionary meaning of morphological variation. In the Mediterranean Basin, wall lizards (*Podarcis* spp.) provide a particularly interesting system for investigating phenotypic variation, with remarkable levels of intraspecific morphological variation and cryptic diversity. Several studies in this group have investigated variation in morphology and performance, and their relationship, both in relation to habitat and focusing on sexual dimorphism (Van Damme et al. 1997; Brecko et al. 2008; Kaliontzopoulou et al. 2012, 2013; Gomes et al. 2016). From an ecomorphological perspective, habitat use has been shown to be an important determinant of macroevolutionary phenotypic differentiation in head shape but not in body size or limb length in wall lizards, although patterns differed between the sexes (Kaliontzopoulou et al. 2015). At the intraspecific level, both limb and head morphology are known to differ across different habitat types of *P. bocagei*, but again the degree of differentiation between sexes varies between habitats, suggesting an interaction between natural and sexual selection (Kaliontzopoulou et al. 2010a). Interestingly, some of the morphological patterns retrieved in that study aligned with, while others contradicted, predictions of the ecomorphological paradigm, raising questions about the functional, and therefore evolutionary, significance of the observed variation.

Indeed, morphological differentiation does not always translate into functional variation, and the evidence available is frequently contradictory. In the context of sexual dimorphism, differences in morphology between males and females of *P. melisellensis* translate into different bite force capacities, but not different sprint speeds (Brecko et al. 2008). By contrast, two Iberian *Podarcis* wall lizards have been reported to differ in head morphology but this differentiation did not translate into bite force capacity, suggesting that ecological variation between species was only reflected on morphology but not on functional capacities (Kaliontzopoulou et al. 2012). In the case of locomotor performance, some studies have provided evidence of an association between morphological traits and locomotor performance (Kaliontzopoulou et al. 2013), but others have failed to detect this association (Van Damme et al. 1997; Vanhooydonck et al. 2000; Gomes et al. 2016). Thereby, it is not clear whether morphological evolutionary responses to habitat and sexual dimorphism are mediated by functional performance and, if so, which traits are involved and which is the exact link between morphology and function (Irschick et al. 2008).

In this study, we investigate how natural and sexual selection may contribute in shaping morphological traits and performance differently given the surrounding environment, at the intraspecific level. For this purpose, we selected populations of *P. bocagei* from two contrasting habitat types, representing saxicolous and ground-dwelling ecological habits. We tested whether individuals from different habitats differ in locomotor and biting performance, as we would expect under predictions of the ecomorphological paradigm. Further, we investigated to what extent and how individual variation in morphology translates into variation in functional performance, as predicted by biomechanical rules and as suggested by studies in other lizard groups. Based on previous observations on the morphology and ecology of this species, and considering ecomorphological patterns in other lizards, we hypothesize that individuals from dunes, which are generally ground-dwelling, have little chance to climb, live in more open habitats, and have higher and more rounded heads and longer limbs, will exhibit stronger bites and will be better sprinters. On the other hand, we expect individuals from agricultural walls, which have been generally considered as saxicolous, frequently using vertical surfaces and have flattened head and shorter limbs, to perform better when climbing and possibly exhibit reduced biting performance, as a result of physical constraints on head height. In addition, considering the well-known existence of male-biased sexual dimorphism in these lizards, we expect that males will exhibit stronger biting and locomotor performance. Finally, given that the ground-dwelling populations studied here are known to be morphologically more dimorphic than saxicolous ones (Kaliontzopoulou et al. 2010a), we were interested in investigating if this variation also translates into differences in the degree of sexual dimorphism in whole-organism performance between habitats. The mechanical constraints imposed by a saxicolous life translated in a less pronounced sexual dimorphism than in the animals living in open environments (Kaliontzopoulou et al. 2010a), and may lead to differences in functional capacities.

Material and methods

Study organism

Podarcis bocagei is a lacertid lizard endemic to the NW Iberian Peninsula, and it can be found in a variety of habitats: sandy areas with or without rocks, sparse vegetation, and stone walls that delimit agricultural fields (see e.g., Kaliontzopoulou et al. 2010a). Lizards for this study were captured in four localities: two dune areas (Madalena and Mindelo) and two sites with agricultural stone walls (Gião and São Mamede do Coronado). We collected a total of 156 adult individuals, including 76 females and 80 males (approximately 20 males and 20 females from each population), by noosing (García-Muñoz and Sillero 2010) in October 2012. Lizards were placed in cloth bags, transported to the laboratory, and housed in individual terraria, where they were fed with live mealworms and provided with water ad libitum. Before experiments, animals were allowed to rest for two days to ensure acclimation. After the conclusion of laboratory experiments, all individuals were released back to the site where they had been captured. We performed all experiments in autumn, that is, in the advanced post-reproductive season (Carretero et al. 2006), to exclude any potential effects of pregnancy on female performance (Bauwens and Thoen 1981) or due to low body condition immediately after reproduction on both sexes (Galán 1996).

Quantified parameters

In all individuals captured, we measured the following linear biometric traits: snout-vent length (SVL), trunk length (TRL), head length (HL), head width (HW), head height (HH), mouth opening (MO), forelimb length (FLL), and hind limb length (HLL), using electronic calipers (precision ± 0.01 mm; see Kaliontzopoulou et al. 2007 for a detailed description of variables). All morphological traits were ln-transformed for further analyses.

All experiments to quantify functional performance and examine microhabitat selection were carried out at a room temperature of about 31 °C, which is approximately the selected body temperature of the species (Amaral et al. 2012). Prior to and in between trials, lizards were placed for at least 1 h in a terrarium exposed to an infrared lamp of 150 W, allowing them to thermoregulate and attain their preferred body temperatures (Veríssimo and Carretero 2009).

For all individuals, three types of locomotor performance were measured (Kaliontzopoulou et al. 2013): sprint speed (SPR), climbing capacity (CLI), and maneuverability (MAN). Sprint speed on a horizontal surface was measured by chasing animals along a 1-m-long and 15-cm-wide racetrack, with a cork substrate (Van Berkum et al. 1989; Braña 2003). Climbing capacity was quantified by chasing animals up a similar racetrack, tilted to an angle of 60°. Cork was used as a substrate because it provides very good traction (Van Damme et al. 1997). To quantify maneuverability, a 0.5-m-long and 15-cm-wide pinboard was placed on the racetrack. This pinboard was made of 8-mm diameter pins placed at equal distances of 35 mm (Vanhooydonck et al. 2000). We allowed a rest of at least 2 h between trials to ensure physical recovery of the individuals. All trials were filmed with a digital camera (Canon EOS 60D) at a filming speed of 50 frames per second. Locomotor speed in the three types of racetracks was measured on different days, and the order in which animals were subjected to the tests was randomized. Each individual was tested three times in each type of racetrack to ensure that maximal locomotor capacity was recorded. Each run was scored as "bad" or "good," and the "bad" races, in which the animals turned around during the race, were eliminated (sensu Van Berkum and Tsuji 1987; Tsuji et al. 1989). The position of the lizard across each run was digitized using MaxTRAQ 2D motion analysis software (Innovision Systems Inc. 2009). The highest instantaneous speed (Gomes et al. 2017) recorded across the three trials was taken as an estimate of each animal's maximum performing capacity in each of the three types of racetrack and log-transformed for further analyses.

Bite force was measured using an isometric Kistler force transducer (type 9203, Kistler Inc., Winterthur, Switzerland) mounted on a vertical holder and connected to a Kistler charge amplifier (type 5058A, Kistler Inc., Winterthur, Switzerland). Bite force measurements were obtained by provoking the lizard to bite a pair of thin metal plates connected to the force transducer (see Herrel et al. 2001a for a detailed description). The tip of the metal plates where the lizard bit was delimited with a marker to ensure all lizards bit at an equal distance from the revolving arms and thus standardize the point of force exertion. Each lizard was tested five times to ensure that the maximal individual bite force per individual was registered. The maximum bite force measure per individual was retained and log-transformed for further analyses.

Statistical analyses

To represent total head size (HS), we used the scores of the first principal component calculated using HL, HW, HH, and MO. For this purpose, principal components of the covariance matrix of head dimensions were calculated using the function prcomp of stats package (R Development Core Team 2016). The four head dimensions had similarly high loadings of the same sign (MO, 0.52; HH, 0.50; HW, 0.49; and HL, 0.49) on the first principal component, which explained 91% of total variance, and was therefore taken to represent HS. To investigate if there were differences between habitats and sexes in size, we used an ANOVA comparison. Next, ANCOVA models were run using each measured morphological trait as the response variable, and habitat (HAB), population nested within habitat (POP), sex, and interaction terms (HAB×SEX and POP×SEX) as predictors, and SVL as a covariate. To examine whether habitats and sexes differed in locomotor performance, we performed ANOVA comparisons on each type of locomotor speed and bite force performance separately, with the same design as for morphology. We also performed ANCOVA comparisons on each type of locomotor speed and bite force performance separately with the same design and considering SVL—in the case of locomotor performance—and HS—in the case of bite force—as covariates. Throughout, we always used permutation-based ANOVA procedures using 1000 randomizations of Euclidean distance matrices as implemented in the adonis function of the vegan R-package (Oksanen et al. 2012).

To investigate the multivariate association between morphology and performance, we used two-block partial least-squares regression (PLS) as implemented in the plsr function of the pls R-package (Mevik et al. 2011). To investigate the association between morphology and locomotor performance (three variables: SPR, CLI, MAN), we only used head size and limb and trunk variables, as these traits are known to determine locomotor performance in these and other lizard species (Kaliontzopoulou et al. 2010a, 2013; Vanhooydonck and Van Damme, 2001 Cameron et al. 2013; Gomes et al. 2016). We first performed the PLS with raw variables, and then we repeated the analysis after correcting all locomotor performance and morphological variables for size effects through a regression on SVL. In the case of the association between morphology and biting performance, we only have one performance variable; however, we used two-block partial least-squares regression to be concordant with the previous analysis of locomotor performance. We only used head dimensions (HL, HW, HH, and MO), which are the main morphological determinants of bite force (e.g., Herrel et al. 2001a; Kaliontzopoulou et al. 2012). Similar to the approach for locomotor performance, we first performed the PLS with raw variables and then we re-run the analysis after size-correcting both bite performance and morphological variables through a regression on HS.

All statistical analyses were performed using R v. 3.3.1 (R Development Core Team 2016).

Results

ANOVA comparisons indicated that individuals from different habitats differed in size ($F = 8.135$, $p = 0.007$), where animals from dunes were larger in body size. ANCOVA comparisons using SVL as the covariate only revealed significant differences between habitats in relative head height, where individuals from dune environments had relatively higher heads than those from walls. ANCOVA also confirmed significant differences between the sexes in all morphological traits, where males had longer limbs and larger heads, but shorter trunks than females (Table 1).

ANOVA comparisons on locomotor performance showed that individuals from walls exhibited higher climbing capacities (Table 2, Fig. 1). Sex did not have a significant effect on locomotor performance. We also detected significant differences between population in sprint capacity. Furthermore, a significant interaction between habitat and sex was identified, where individuals of both sexes from walls exhibited similar locomotor performance, whereas in dunes, males were better climbers then females. ANCOVA comparisons using SVL as the covariate revealed a significant effect of body size on locomotor performance, but differences between habitats and the interaction between habitat and sex remained significant for climbing after accounting for variation in body size (Table 3, Fig. 1). ANOVA comparisons also showed that lizards from dunes bit harder than those from walls. Bite force was also significantly different between the sexes, where males attained a higher maximal bite force than did females (Table 2, Fig. 2). Finally, ANCOVA comparisons using HS as the covariate revealed a significant effect of head size on bite performance, and differences between habitats were still significant after accounting for variation in head size, and also differences between the sexes remained, at least in dunes (Table 3, Fig. 2).

Table 2 Results of ANOVA comparisons performed on each type of locomotor speed and bite force separately to examine the effect of habitat (HAB), population nested within habitat (POP), sex, and their interaction in Bocage's wall lizard—*P. bocagei*

		SPR	MAN	CLI	Bite
HAB	*F*	0.689	1.773	9.783	6.49
	p	0.419	0.187	**0.003**	**0.018**
SEX	*F*	1.117	1.035	3.068	81.123
	p	0.304	0.291	0.07	**0.001**
POP	*F*	10.771	2.184	2.689	0.927
	p	**0.001**	0.127	0.071	0.381
HAB×SEX	*F*	2.562	1.131	4.485	0.113
	p	0.132	0.252	**0.03**	0.716
POP×SEX	*F*	1.451	0.216	1.987	0.791
	p	0.26	0.839	0.139	0.476

Significant effects are marked in bold. See "Material and methods" for variable abbreviations

F, F-statistic; *p*, corresponding *p* value

Two-block partial least-squares regression revealed a significant association between trunk and limb morphology and locomotor performance ($r = 0.305$ and $p = 0.001$), where higher speeds are associated with longer trunks and limbs and smaller head size (Fig. 3). However, after size-correcting all variables, the significant association between morphological traits and locomotor performance

Table 1 Results of ANCOVA comparisons performed on each linear measurement separately with habitat (HAB), population nested within habitat (POP), and sex as predictors, and SVL as a covariate in Bocage's wall lizard—*P. bocagei*

		HL	HW	HH	MO	FLL	HLL
SVL	*F*	536.69	954.88	447.83	1130.57	508.69	758.89
	p	**0.001**	**0.001**	**0.001**	**0.001**	**0.001**	**0.001**
HAB	*F*	0.43	0.61	7.94	0.2	0.31	0.05
	p	0.503	0.432	**0.008**	0.643	0.551	0.826
SEX	*F*	209.35	349.7	112.12	462.35	193.41	412.58
	p	**0.001**	**0.001**	**0.001**	**0.001**	**0.001**	**0.001**
SVL×HAB	*F*	0.3	0.42	0.01	4.66	0.36	0.42
	p	0.6	0.518	0.907	0.034	0.532	0.528
SVL×SEX	*F*	6.75	23.13	12.83	24.54	11.73	22.54
	p	**0.014**	**0.001**	**0.001**	**0.001**	**0.002**	**0.001**
HAB×SEX	*F*	2.3	0.001	0.71	0.44	0.01	1.73
	p	0.137	0.979	0.386	0.482	0.922	0.169
SVL×POP	*F*	1.28	6.02	11.23	0.63	0.7	0.79
	p	0.273	**0.007**	**0.001**	0.544	0.487	0.458
SVL×HAB×SEX	*F*	1.77	0.12	0.23	0.47	0.01	0.02
	p	0.197	0.733	0.656	0.505	0.919	0.894
SVL×POP×SEX	*F*	4.38	2.92	1.77	0.53	0.8	3.34
	p	**0.013**	0.058	0.128	0.6	0.471	**0.038**

Significant effects are marked in bold. See "Material and methods" for variable abbreviations

F, F-statistic; *p*, corresponding *p* value

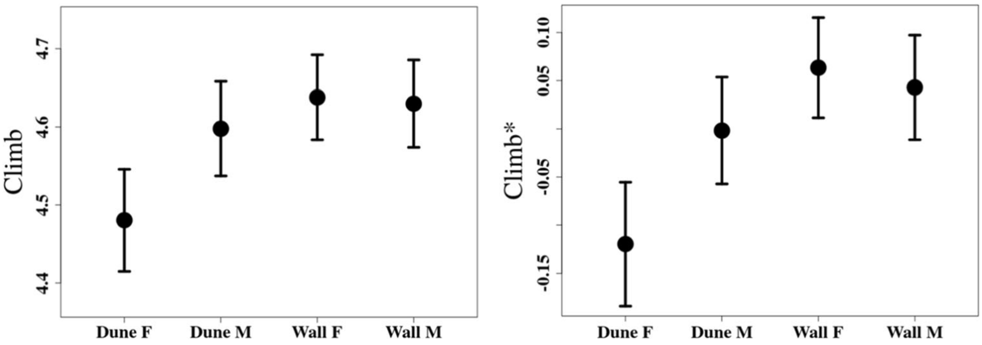

Fig. 1 Variation across groups of Bocage's wall lizard—*P. bocagei*—in climbing speed (left), and climbing speed corrected for SVL (right). Points represent means, and vertical bars denote 95% confidence intervals. Dune F, females from dunes; Dune M, males from dunes; Wall F, females from walls; and Wall M, males from walls

was lost ($r = 0.135$ and $p = 0.565$). Two-block partial least-squares regression also revealed a significant association between head morphology and bite performance ($r = 0.968$ and $p = 0.001$), where higher bite forces are associated with larger head dimensions (Fig. 4). This association remained significant after taking head size effects into account ($r = 0.365$ and $p = 0.001$), where relatively higher bite forces were associated with relatively wider and flatter heads, and with relatively longer jaws (Fig. 4).

Table 3 Results of ANCOVA comparisons performed on each type of locomotor speed and bite force performance separately with habitat (HAB), population nested within habitat (POP), and sex as predictors, and SVL (in the case of locomotion) or HS (in the case of bite) as a covariate (represented by X) in Bocage's wall lizard—*P. bocagei*

		SRP	MAN	CLI	Bite
X	*F*	14.911	2.308	8.908	2344.48
	p	**0.001**	0.124	**0.003**	**0.001**
HAB	*F*	3.182	2.969	16.134	3.867
	p	0.069	0.082	**0.001**	**0.048**
SEX	*F*	0.637	0.784	2.361	10.279
	p	0.414	0.368	0.118	**0.003**
X×HAB	*F*	1.939	0.328	0.25	0.572
	p	0.166	0.549	0.625	0.451
X×SEX	*F*	1.159	0.024	1.518	0.358
	p	0.259	0.882	0.23	0.548
HAB×SEX	*F*	2.828	1.343	5.085	0.686
	p	0.089	0.255	**0.024**	0.415
X×POP	*F*	9.409	1.814	2.348	1.085
	p	**0.001**	0.148	0.105	0.332
X×HAB×SEX	*F*	2.761	1.532	0.416	0.852
	p	0.123	0.234	0.508	0.37
X×POP×SEX	*F*	1.215	0.434	1.941	0.025
	p	0.305	0.606	0.132	0.974

Significant effects are marked in bold. See "Material and methods" for variable abbreviations

F, F-statistic; *p*, corresponding *p* value

Discussion

Our investigation of how functional performance mediates the evolutionary response of morphology to habitat revealed fast-evolving ecomorphological variation among populations of *Podarcis bocagei*, where a direct association existed between head morphology and bite performance. However, we could not establish links between limb morphology and locomotor performance at the individual level after correcting for size effects. Nevertheless, significant differences in climbing capacity existed between habitats, where individuals from walls were better climbers than those from dunes, suggesting a very fast evolutionary response of functional performance to habitat use, identifiable at the intraspecific level. Interestingly, a significant interaction between habitat and sex was detected in climbing performance. The same was the case for biting performance, although sexual differentiation was definitely the main factor driving variation in head functional morphology. Taking into account all the results, we found a complex interaction between natural and sexual selection on whole-organism performance, which are, in some cases, reflected on morphological variation. This complex interaction between different types of selective mechanisms results in context-dependent combined variation of morphological and performance traits, which sometimes confirms the ecomorphological paradigm and other times contradicts it.

Form-function associations

Indeed, under the ecomorphological paradigm, an association is predicted between morphology and performance as a response to different selective forces imposed by the environment, i.e., habitat structure in this study. However, here, we observe a complex pattern: we could detect an association between head morphology and bite force, but not between limb morphology and locomotor performance after correcting for size effects. Both pairs of functional morphology sets—head-biting and limbs-locomotion—are commonly associated as a response to environmental factors in lizard species (Losos and Sinervo 1989; Sinervo and Losos 1991; Melville and Swain 2000; Herrel et al. 2001b, Irschick et al. 2005b,

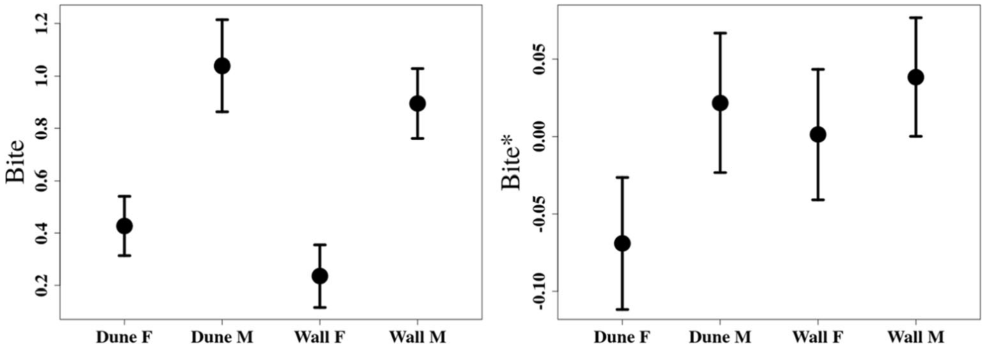

Fig. 2 Variation across groups of Bocage's wall lizard—*P. bocagei*—in bite force (left) and bite force corrected for HS (right). Points represent means, and vertical bars denote 95% confidence intervals. Dune F, females from dunes; Dune M, males from dunes; Wall F, females from walls; Wall M, males from walls

Kaliontzopoulou et al. 2013), but cases where this association was not found are also known (Vanhooydonck et al. 2000; Goodman et al. 2008), including several examples in *Podarcis* lizards (Van Damme et al. 1997; Vanhooydonck et al. 2000; Brecko et al. 2008; Kaliontzopoulou et al. 2012; Gomes et al. 2016). This lack of the typical functional morphological pattern in the locomotor system could be explained by factors other than limb length regulating locomotor performance, such as physiology, behavior, or biochemistry, or even by other morphological and locomotor traits not examined in this study being more relevant (Van Damme et al. 1997; Jayne and Irschick 1999; Braña, 2003; Revell et al. 2007; Vervust et al. 2007).

In the case of bite force, our results suggest an association with head morphology, which is largely driven by size effects and sexual size dimorphism (Fig. 4, left). However, after taking size effects into account, we see that head height (negative correlation) and head width and mouth opening (positive correlation) are the traits that may constrain bite force (Fig. 4, right). Following biomechanical rules and a common pattern in lizards and other organisms (Herrel et al. 2001a, b, 2005; Thomas et al. 2015), two-block partial least-squares regression suggests that higher bite forces are associated with relatively wider heads (Fig. 4). However, we also observed a negative correlation between head height and bite force, where individuals with relatively flatter heads had higher bite forces than those with relatively higher heads, a pattern that disagrees with predictions of biomechanical models of biting in lizards. It has been demonstrating that high bite forces are associated with wider and taller heads in several organisms (e.g., Herrel et al. 2001a, b, 2005; Thomas et al. 2015), indicating that external head measures are not good predictors of

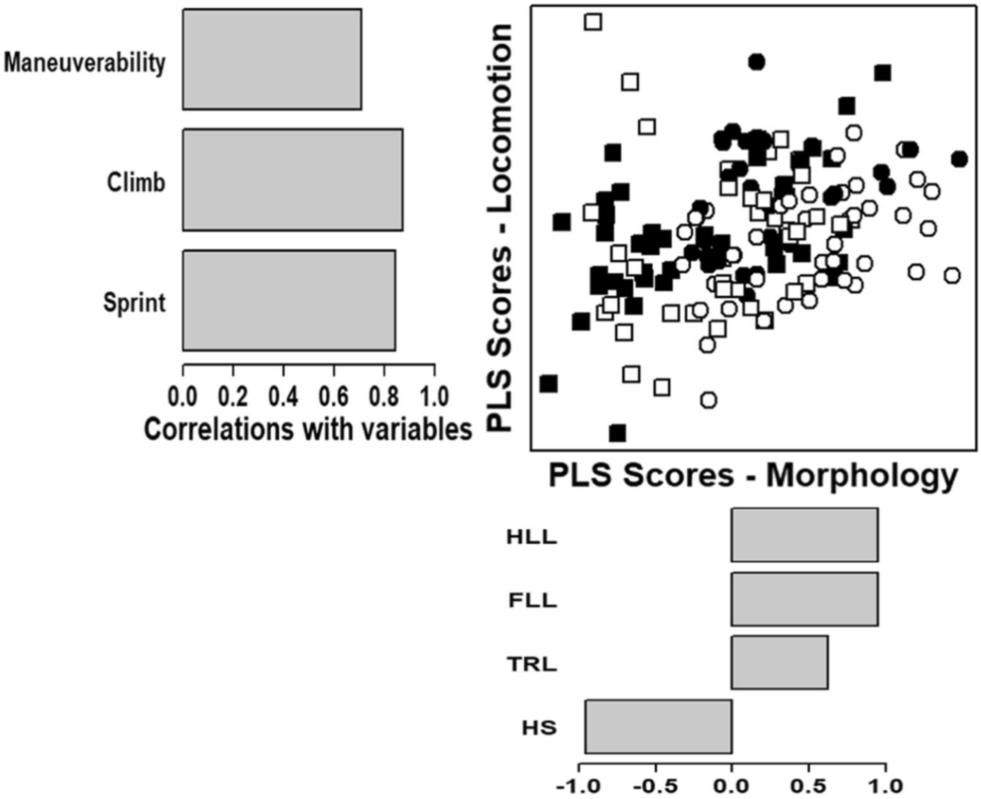

Fig. 3 Scatter-plot of individual Bocage's wall lizard—*P. bocagei*—scores of dune individuals (black squares, males; black circles, females) and wall individuals (white squares, males; white circles, females) obtained from partial least-squares (PLS) analysis between morphology (trunk length, TRL; forelimb length, FLL and hind limb length, HLL; and head size, HS) and locomotor performance (sprint, climb, maneuverability)—variables not corrected by size. Bar-plots next to morphology axis represent the correlations observed between that axis and locomotor performance

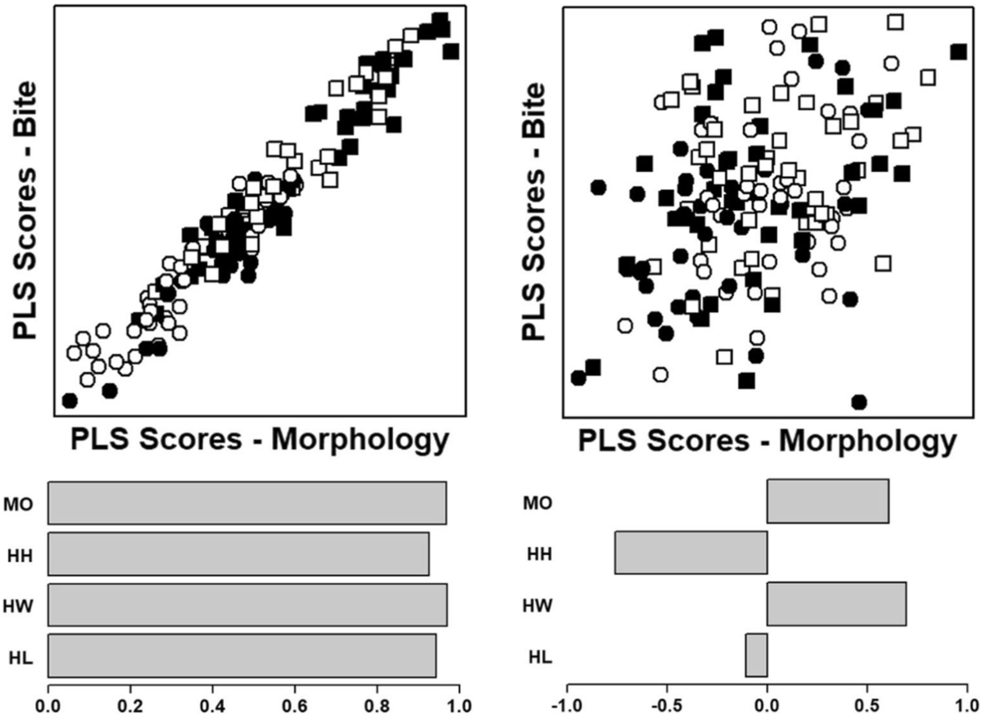

Fig. 4 Scatter-plot of individual Bocage's wall lizard—*P. bocagei*—scores of dune individuals (black squares, males; black circles, females) and wall individuals (white squares, males; white circles, females) obtained from partial least-squares (PLS) analysis between head morphology (head length, HL; head width, HW; head height, HH; mouth opening, MO) and bite force—left, variables not corrected by head size; right, variables corrected by head size. Bar-plots next to morphology axis represent the correlations observed between that axis and bite force

the pattern observed and other factors as internal muscle composition should be studied. Our results are in accordance with the known pattern of sexual dimorphism in *Podarcis bocagei* and other lizards, where males are larger in total body size, with relatively larger heads and more robust head shapes (Kaliontzopoulou et al. 2008), a pattern also known to translate into higher bite forces (Herrel et al. 2001a, b; Kaliontzopoulou et al. 2012). Higher bite performance in males is known to be associated with male dominance (Herrel et al. 1999; Husak et al. 2006; Huyghe et al. 2009), an advantage in antagonistic behavior between males for territory defense and/or mate acquisition and/or an advantage during copulation (Lappin and Husak 2005). The morphology-performance axis aligns with sexual differentiation (Fig. 4), pointing to sexual selection as a major force driving the joint phenotypic differentiation of head morphology and function; however, natural selection related to habitat type also seems to play a role in shaping whole-organism performance.

Functional morphological responses to habitat variation

The investigation of performance across habitats revealed that lizards from dunes bite harder than those from walls (Table 2, Fig. 2), as is expected given the larger body size observed in dune populations, and provided that animals with larger heads bite harder (Herrel et al. 2001a, b). Interestingly, however, when body size effects were taken into account, we found that animals from walls bite harder relative to their head size than those from dunes (Table 3, Fig. 2). This result indicates that the small head size observed in walls does not have repercussions on bite performance. Thereby, the potential physical constraints imposed by saxicolous habits—i.e., smaller heads being favorable in rocky environments to facilitate the use of small holes and rock crevices for refuge (Vitt et al. 1997; Revell et al. 2007)—do not influence bite force performance. A potential explanation for this pattern is different osteology and/or different jaw muscle insertion, orientation, or even length across habitats (Herrel et al. 1996, 1998, 2001b; Lappin et al. 2006; Huyghe et al. 2009). Indeed, this is a very feasible explanation, which merits further attention in future studies, as the feeding apparatus is known to evolve very fast in wall lizards, exhibiting remarkable short-term responses to selection pressures (Herrel et al. 2008). In fact, this observation adds to the evidence suggesting that this flexibility in the relationship between head morphology and function to maintain biting performance is common in *Podarcis*, both within and across species (Herrel et al. 1996; Kaliontzopoulou et al. 2012). As such, a type of many-to-one mapping of morphology on function seems like a plausible mechanism for balancing the requirements posed by natural (habitat use) and sexual selection (Alfaro et al. 2005).

By contrast to this maintenance of biting functionality despite contrasting ecological demands across habitats, locomotor performance capacities seem to align more to expectations (Table 2, Table 3, Fig. 1), we found that animals from walls were faster climbers than those from dunes. Here, natural selection seems to act upon these animals increasing their ability to climb. In other words, lizards from agricultural walls adapt to their natural environment by increasing their climbing speed, which enhances their probability of survival, while escaping from predators in perpendicular surfaces. Several other studies have provided evidence of a clear and strong association between habitat use and performance capacities across species (e.g., *Anolis*: Losos 1990a, b; Irschick and Losos 1999; Elstrott and Irschick 2004, subfamily Lygosominae: Melville and Swain 2000; Goodman et al. 2008, or other systems: Vanhooydonck and Van Damme 2003; Vanhooydonck et al. 2005; Tulli et al. 2011). The results obtained here support the idea that this kind of association can evolve quite fast, being detectable at the microevolutionary level, i.e., among a set of geographically nearby, genetically quite uniform populations of the same species (Pinho et al. 2011). As such, the pattern of differentiation in climbing performance described here represents a very fast functional response to habitat type, occurring in a time frame of about 10,000 years (Pinho et al. 2011). Such a fast, fine-scale response could be facilitated by proximate mechanisms like phenotypic plasticity or differential growth in different habitats, as is known to occur in the locomotor apparatus of other lizard groups (Losos et al. 2000; Kolbe and Losos 2005). Given the high flexibility of ontogenetic trajectories observed across *Podarcis* wall lizards (e.g., Kaliontzopoulou et al. 2010b; Piras et al. 2011), this seems like a reasonable hypothesis, which would need to be further explored experimentally in future studies.

Despite this positive, short-frame association between habitat use and locomotor performance, we also found some unexpected results. Specifically, taking into account several interspecific studies that showed an association between morphology, performance, and habitat use to understand better how natural selection shape whole-organism (e.g., Losos 1990a, b; Irschick and Losos 1999: Melville and Swain 2000; Vanhooydonck and Van Damme 2003; Elstrott and Irschick 2004; Vanhooydonck et al. 2005; Goodman et al. 2008; Tulli et al. 2011), we had predicted that lizards from dunes would be better sprinters than those from walls. However, a differentiation between the two types of habitats in sprint speed was not identifiable in our data. This reduced functional differentiation between habitat types in locomotor performance, which is the "classical" trait expected to vary due to its direct connection to structural habitat, could be a matter of scale, as at the sampled populations are geographically very close, allowing extensive gene flow between them, and they are known to share the most important part of their evolutionary background, being genetically quite uniform (Pinho et al. 2011).

Alternatively, individuals from walls may adapt to moving on inclined surfaces by increasing their climbing capacity, but at the same time maintain their ability to sprint in horizontal surfaces, which is still beneficial given the generally ground-dwelling habits of this species. Indeed, horizontal sprinting is associated with escape from predators (Husak and Fox 2006; Miles 2004) and it should be still under selection in environments where agriculture walls are predominant. In fact, lizards in such environments also escape from predators by sprinting horizontally on top of the walls or by jumping to the ground and sprinting to hide within the adjacent vegetation cover (personal observation). Indeed, *P. bocagei* is quite generalistic in its ecological habits (i.e., sensu Kaliontzopoulou et al. 2015) and maintain a high degree of flexibility in terms of habitat preference. Despite the marked contrast of habitat structure in the localities of origin of the studied populations, individuals did not exhibit differences in the main aspects of microhabitat choice under experimental conditions (Supp. Inf.). This observation suggests that, although morphology and functional performance vary across populations, a global flexibility is also maintained, reinforcing the possibility of an important role for phenotypic plasticity in mediating the observed patterns. Particularly in view of the lack of an association between locomotor performance and morphology observed here, it seems that climbing performance can be enhanced in saxicolous populations through mechanisms (e.g., physiology: Braña, 2003; behavior: Van Damme et al. 1997) which do not influence the capacity of the lizards to also maintain their sprinting performance. In fact, this lack of a trade-off between sprinting and climbing seems to be a recurrent pattern, which occurs at several evolutionary levels in lacertids, including populations of the same species (i.e., results presented here), lineages of the same species complex (Van Damme et al. 1997), and deeply differentiated species at the family level (Vanhooydonck and Van Damme 2001).

Interactions between natural and sexual selection

We have seen how sexual and natural selection shape functional and morphological diversity separately. However, the balance between both selective forces is complex and in this study result in differences in the degree of functional sexual dimorphism between habitats (Table 1, Table 2, and Table 3). Our results on climbing performance showed that individuals from dune habitats were more dimorphic than those inhabiting agriculture walls (Fig. 1). This is in accordance with the variation in the degree of morphological sexual dimorphism between different habitats previously reported for *P. bocagei* (Kaliontzopoulou et al. 2010a). While the same morphological pattern was not detected here, most probably due to the lower number of populations and individuals examined, we did identify differences between habitats in the degree of sexual differentiation in climbing capacity. The fact that individuals of the two sexes living in walls had similar climbing performance could be explained by the necessity of both sexes to escape from predators in inclined surfaces. By contrast, individuals from dunes (ground-dwelling) have less of a selective pressure in this direction, and exhibit a more pronounced difference between sexes in their climbing capacities, possibly associated to behavioral differences related to their social roles. Here, males, which normally have larger home ranges to patrol (Stamps 1983; Perry and Garland 2002; Diego-Rasilla and Perez-Mellado 2003), and move more extensively in search of mating opportunities, may benefit more by enhanced climbing capacities, while females seem more limited in this respect (Fig. 1). Nevertheless, such a hypothesis should be further investigated in the future.

Put together, the results obtained here highlight the potential for remarkable flexibility in morphology-function associations, and their potential for responding to environmental variation in very short evolutionary time intervals. This means that establishing whether morphological variation is associated with habitat use through influences on whole-organism performance, as dictated by the ecomorphological paradigm, is not necessarily straightforward, even using data on individuals at the intraspecific level. Interestingly, both the head-bite and limbs-locomotion functional systems seem to be quite flexible in wall lizards, but in different directions. In one case—bite performance—the same whole-organism performance capacities can be maintained despite varying external morphological properties. In the second case—locomotor performance—different performance capacities are achieved by individuals with similar morphological properties. This suggests that these lizards exhibit a particularly high complexity of the morphology-performance association, through the interference of other regulatory mechanisms such as muscle orientation, physiology, behavior, etc. Such complexity may uncouple performance and morphology and provide an explanation for success of this species in the ecosystems of NW Iberia, and also explain their potential for exhibiting extreme levels of intraspecific morphological variability. In this sense, morphology does not seem to be canalized through its integration with functional performance (sensu Klingenberg 2014), and as functionality can be maintained through other properties, external morphology is relatively free to vary. Further studies investigating the ecological significance of performance are required to fully understand how, and at which hierarchical level, these organisms' phenotypic traits respond to environmental variation. For this, investigating how lizards implement their maximal performance to perform different ecological and social tasks is important to understand their true evolutionary potential (Irschick et al. 2005c; Husak 2006).

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