Acta Oecologica 70 (2016) 87–95

Contents lists available at ScienceDirect

Acta Oecologica

journal homepage: www.elsevier.com/locate/actoec

Original article

The relevance of morphology for habitat use and locomotion in two species of wall lizards

Verónica Gomes [a], [b], [*], Miguel A. Carretero [a], Antigoni Kaliontzopoulou [a]

[a] CIBIO Research Centre in Biodiversity and Genetic Resources, InBIO, Universidade do Porto, Campus Agrário de Vairão, Rua Padre Armando Quintas, Nº 7. 4485-661 Vairão, Vila do Conde, Portugal
[b] Departamento de Biologia da Faculdade de Ciências da Universidade do Porto, Porto, Portugal

ARTICLE INFO

Article history:
Received 4 August 2015
Received in revised form
1 December 2015
Accepted 2 December 2015
Available online xxx

Keywords:
Morphology
Habitat
Performance
Lizards

ABSTRACT

Understanding if morphological differences between organisms that occupy different environments are associated to differences in functional performance can suggest a functional link between environmental and morphological variation. In this study we examined three components of the ecomorphological paradigm – morphology, locomotor performance and habitat use – using two syntopic wall lizards endemic to the Iberian Peninsula as a case study to establish whether morphological variation is associated with habitat use and determine the potential relevance of locomotor performance for such an association. Differences in habitat use between both lizards matched patterns of morphological variation. Indeed, individuals of *Podarcis guadarramae lusitanicus*, which are more flattened, used more rocky environments, whereas *Podarcis bocagei*, which have higher heads, used more vegetation than rocks. These patterns translated into a significant association between morphology and habitat use. Nevertheless, the two species were only differentiated in some of the functional traits quantified, and locomotor performance did not exhibit an association with morphological traits. Our results suggest that the link between morphology and habitat use is mediated by refuge use, rather than locomotor performance, in this system, and advise caution when extrapolating morphology-performance-environment associations across organisms.

1. Introduction

Whether or not, and how, organisms adapt to their environment are two central questions in ecology, evolution and conservation biology (Aerts et al., 2000; Arnold, 1998; Collar et al., 2010; Elstrott and Irschick, 2004; Kaliontzopoulou et al., 2010a). Different climatic, structural and biotic characteristics of the environment may impose ecological pressures on organisms, and mould phenotypic evolution and morphological diversification (Irschick and Garland, 2001; Ricklefs et al., 1981; Vitt et al., 1997). To start understanding the potential evolutionary meaning of morphological variation, we need to evaluate whether specific traits increase the functional capability of an organism (Arnold, 1983; Garland and Losos, 1994). This is usually done in the framework of the ecomorphological paradigm, where differences in morphology are expected to be associated with different ecological performance capacities (e.g. maximum sprint speed), which in turn translate into variation in fitness among individuals in a given environment (Arnold, 1983). Here, selection acts on whole-organism performance to maximise the ability of the individuals to perform certain ecological and social tasks, guarantee their survivorship, and enhance their reproductive success, with correlated effects on morphological characters of biomechanical relevance for these functions (Irschick et al., 2008). Because the functional challenges that organisms face vary across environments, this type of microevolutionary process eventually leads to an association between morphological and environmental variation. As such, establishing whether morphological differences among organisms that occupy different environments are reflected into differences in functional performance can help us to disentangle the complex relationship between traits that culminate in differences in fitness and enhance our understanding of the underlying evolutionary mechanisms (Irschick and Garland, 2001; Irschick et al., 2005a; Miles, 2004; Vanhooydonck and Van Damme, 2001).

---

[*] Corresponding author. CIBIO Research Centre in Biodiversity and Genetic Resources, InBIO, Universidade do Porto, Campus Agrário de Vairão, Rua Padre Armando Quintas, Nº 7. 4485-661 Vairão, Vila do Conde, Portugal.
E-mail address: veronica.a.s.g@gmail.com (V. Gomes).

http://dx.doi.org/10.1016/j.actao.2015.12.005

Lizards have been extensively used as model organisms for ecomorphological studies because they are present in a great variety of habitats, and they exhibit a wide range of morphologies and locomotor modes (Arnold, 1998; Garland and Losos, 1994; Irschick and Garland, 2001; Irschick, 2002). Numerous studies indicate that different aspects of locomotor performance are ecologically relevant in different structural habitats, as lizards need to move to capture prey, escape from predators, thermoregulate, find mates and defend territories (Garland and Losos, 1994). As such, those lizard species that live in open areas and use sprinting as their main antipredatory strategy are considered as runners, and they are expected to have long hind limbs to enable longer strides; relatively short forelimbs, to avoid interference with the cycling of the hind limbs; and laterally flattened bodies, to enhance lateral flexibility and maximise stride length (Da Silva et al., 2014; Kaliontzopoulou et al., 2010a; Losos and Sinervo, 1989; Melville and Swain, 2000; Vanhooydonck and Van Damme, 2001). In contrast, lizards living mostly in rocks are considered as climbers, and they are expected to have shorter limbs and dorsally flattened bodies, to lower the centre of gravity closer to the substrate (Da Silva et al., 2014; Kaliontzopoulou et al., 2010a; Melville and Swain, 2000; Sinervo and Losos, 1991; Van Damme et al., 1997; Vanhooydonck and Van Damme, 2001). Therefore, traits that are favoured in one microhabitat preference may conflict with those that are beneficial in another (Clemente et al., 2013).

Podarcis wall lizards from the Iberian Peninsula and North Africa form a monophyletic clade and they are considered a cryptic species complex (i.e. *Podarcis hispanica* species complex: Kaliontzopoulou et al., 2011; Kaliontzopoulou et al. 2012a). In NW Iberia, we encounter two endemic forms – *Podarcis bocagei* and *P. guadarramae lusitanicus* (Geniez et al., 2014; previously treated as *P. hispanica* type 1A, see Kaliontzopoulou et al., 2011). These two sister forms are particularly interesting from an ecomorphological perspective because, unlike most other members of the group, their distributions overlap widely, both at a wide and local geographic scale (Carretero, 2008; Kaliontzopoulou et al., 2011). Further, despite being sister taxa, both forms markedly differ in body shape, whereby *P. bocagei* has relatively longer limbs, and a higher and more rounded head compared to *P. g. lusitanicus* (Galán, 1986; Kaliontzopoulou et al., 2012b; Pérez-Mellado, 1980). It has been suggested that these differences in body shape reflect different habitat preferences, where *P. g. lusitanicus* is highly saxicolous (Galán, 1986; Gosá et al., 1986; Pérez-Mellado, 1980; Sá-Sousa et al., 2002), whereas *P. bocagei* is mostly ground-dwelling (Domínguez and Salvador, 1989; Galán, 1986, 1994; Kaliontzopoulou et al., 2012b; Pérez-Mellado, 1980). However, differences in habitat use between the two species have never been formally quantified and the relevance of their potential ecological segregation for their morphological differentiation has never been examined.

In this study, we investigate the three components of the ecomorphological paradigm – morphology, locomotor performance and habitat use – using a community with *P. bocagei* and *P. g. lusitanicus* as a case study to examine whether morphological variation is associated with habitat use and determine the potential relevance of locomotor performance for such an association. For this purpose, we first examine if there are differences in habitat use between both forms, which would suggest that they exploit different ecological resources in terms of structural niche. Further, we test whether both forms differ in locomotor performance, as we would expect under predictions of the ecomorphological paradigm. Finally, we test if individual variation in morphology translates into variation in habitat use and locomotor performance, as suggested by studies in other lizard groups. Based on previous observations on the morphology and ecology of the two species, and considering ecomorphological patterns in other lizards, we hypothesize that *P. g. lusitanicus*, which has been generally considered as saxicolous, will mainly use rocky environments. In addition, if morphological variation bears a functional meaning, we expect *P. g. lusitanicus*, which has a flattened head and shorter limbs, to perform better when climbing. On the other hand, *P. bocagei*, which is generally ground-dwelling, with a much higher and rounded head and longer limbs, is expected to be more flexible in terms of habitat use. Because this species uses different types of habitat including vegetation (Kaliontzopoulou et al., 2012b; Sá-Sousa, 2001), we predict that it might perform equally well under different locomotor conditions.

2. Material and methods

Lizards for this study were captured in the coastal zone near the beach of Moledo (N Portugal coast – 41°50′N, 8°52′W), where *P. bocagei* and *P. g. lusitanicus* are found in syntopy across a sandy area with rocks, sparse vegetation, and agricultural fields delimited by human constructed stone walls. The total area sampled was about 6500 m^2. We collected a total of 121 adult individuals by noosing (García-Muñoz and Sillero, 2010), including 65 animals for studying habitat use and 56 for locomotor performance experiments (see also below).

2.1. Morphological variables

In all individuals captured (i.e.,47 males and 32 females of *P. bocagei*, and 20 males and 22 females of *P. g. lusitanicus*), we measured the following linear biometric traits: trunk length (TRL), head length (HL), head width (HW), head height (HH), fore limb length (FLL) and hind limb length (HLL), using electronic callipers (precision 0.01 mm; see Kaliontzopoulou et al., 2007 for a detailed description of variables). In order to separate size and shape, we calculated the isometric size (SIZE) of each individual by projecting all log-transformed linear measurements on an isometric vector (Kaliontzopoulou et al., 2010a) and used it as a multivariate estimate of total body size. To obtain size-corrected variables representing shape variation, we regressed each linear trait on SIZE and retained the regression residuals (hereafter prjTRL, prjHL, prjHW, prjHH, prjFLL and prjHLL) (Kaliontzopoulou et al., 2010a). Animals used to quantify locomotor performance were also weighted using a digital balance (precision 0.0001 g).

2.2. Habitat use variables

In May 2011, when the activity of lizards is at its maximum, we captured a first set of 48 *P. bocagei* (30 males and 18 females) and 15 *P. g. lusitanicus* (five males and 10 females) in order to perform habitat and microhabitat use observations in the field. For each individual captured, we recorded the exact location of capture, using a high-precision GPS (Trimble GPS GeoExplorer 2008 HX). Each individual was measured to record morphological traits and marked with a unique colour code using non-toxic marker paint, so we could distinguish individuals in the field without capturing them. All the animals were released in the same location of capture.

To record microhabitat and habitat use, we performed normalised transects during seven days and 10 h/day with favourable weather conditions. To ensure that all lizards were observed at different times of the day, and therefore capture the individual variability in habitat use, transects were performed in a random order and allowing at least 1 h and a half between repetitions of the same transect. During these transects, we collected a total of 197 observations for *P. bocagei* (114 for males and 83 for females) and 60 observations for *P. g. lusitanicus* (20 for males and 40 for females) and recorded their associated microhabitat variables. To quantify microhabitat use we recorded the type of substrate where the lizard was observed (SUBS: classified as either walls, rocks, vegetation or soil), the height from the ground at the point of observation (HGR), inclination quantified as the angle between the surface where the individual was observed and the horizontal plane (INC), and the diameter of the rock (ROCKD), when lizards were observed on rocks. We also considered habitat used in the 2 m-diameter area surrounding the point of observation by recording the percentage of bare soil, vegetation and rocks.

Before subsequent statistical analyses, height from the ground and inclination were transformed as $y = \log10\ (x + 0.5)$, rock diameter was logarithmically transformed and all percentages were arcsine-transformed.

2.3. Locomotor performance

In October 2011, we captured a second set of 30 *P. bocagei* (15 males and 15 females) and 26 *P. g. lusitanicus* (15 males and 11 females) in order to quantify locomotor performance. We performed locomotor experiments in the autumn to exclude any potential effects of reproduction (i.e. pregnancy) on female performance (Bauwens and Thoen, 1981). Lizards were placed in opaque cloth bags, transported to the laboratory and housed in individual terraria, where they were fed with live mealworms and provided with water *ad libitum*. All animals were allowed to rest for two days after arrival to the lab to ensure acclimation. All experiments were carried out at a room temperature of about 31 °C, which is approximately the selected body temperature of the two species (Amaral et al., 2012; Carretero et al., 2012). Prior to and in between all performance trials, lizards were placed for at least 1 h in an individual terrarium that was exposed to direct natural light, allowing them to thermoregulate and attain their preferred body temperature.

For all individuals, five types of locomotor performance were measured (Kaliontzopoulou et al., 2013): sprint speed (one type), climbing capacity (three types) and manoeuvrability (one type). Sprint speed (SPR) on a horizontal surface was measured by chasing animals along a 1 m-long and 15 cm-wide racetrack, on a cork substrate (Braña, 2003; Van Berkum et al., 1989). Climbing capacity was quantified by chasing animals up a similar racetrack, with varying substrates and inclination conditions. These included: (1) a cork-substrate racetrack tilted to an angle of 60° (CLI60), (2) a sandpaper-substrate racetrack tilted to an angle of 60° (CLI60s) and (3) a cork-substrate racetrack tilted to an angle of 90° (CLI90). Cork was used as a substrate because it provides very good traction (Van Damme et al., 1997), while the sandpaper provided a surface similar to a granite rock (Goodman, 2007). To quantify manoeuvrability (MAN), 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).

Locomotor speed in the five 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 completely stopped or turned around during the race, were eliminated from the analyses (sensu Tsuji et al., 1989; Van Berkum and Tsuji, 1987).

All trials were filmed with a digital camera (Casio EXILIM EX-F1) at a filming speed of 30 fps. The position of the lizard across each trial was digitized using MaxTRAQ 2D motion analysis software (Innovision Systems Inc., 2009). For each type of racetrack, the highest speed recorded over any 10-cm interval across all repetitions was taken as an estimate of each animal's maximum speed in that racetrack. All data of locomotor performance were logarithmically transformed prior to analyses. After the experiments, all individuals were released in the site of capture.

2.4. Data analyses

Because both species are sexually dimorphic, including the populations in the study site (Kaliontzopoulou et al., 2012a, 2012b, 2013) we included sex as a predictor variable in all statistical analyses conducted. To investigate if there were differences between species and sexes in morphology we used ANOVA procedures. All ANOVA models were run using morphological traits (i.e. SIZE and each size-corrected trait separately) as the response variable, and species, sex and their interaction as predictors.

Concerning microhabitat use, we fitted a log-linear model to examine whether species and sexes were found on different substrates with a different frequency. Additionally, for all continuously represented microhabitat (e.g. HGR, INC, ROCKD) and habitat variables (% of bare soil, vegetation and rocks) we performed permutation ANOVAs using species, sex and their interaction as predictor variables, to evaluate differences between SP × SEX groups. This analysis considered individual observations as independent and therefore encompassed variability within individuals in habitat use. In addition, because some individuals were observed more than once, the same analysis was repeated using a linear mixed-effects model as implemented in the lmer function of the lme4 R-package (Bates et al., 2014) and including individual as a random factor.

To examine whether species and sexes differed in locomotor performance, we performed a MANOVA on the multivariate set of maximal locomotor speeds, and also randomized ANOVA comparisons on each type of locomotor speed separately, with species, sex and their interaction as factors. Subsequently, we performed post-hoc comparisons (Tukey's HSD) to test for differences between pairs of groups. We also performed ANCOVA comparisons on the multivariate set of maximal locomotor speeds to examine the effect of species, sex, and their interaction, while considering SIZE and weight as covariates. We always used (M)ANOVA based on permutations, because sample size varied across groups, which resulted in differences in variance. These were based on 1000 permutations of Euclidean distance matrices as implemented in the adonis function of the vegan R-package (Oksanen et al., 2012). Because multiple comparisons were evaluated simultaneously, we implemented the False Discovery Rate (FDR) procedure to adjust the p-values of statistical tests (Benjamini and Yekutieli 2001). To investigate the multivariate association between morphology and performance, and between morphology and habitat, we used a two-block partial least-squares regression as implemented in the plsr function of the pls R-package (Mevik et al., 2011). To investigate the association between morphology and locomotor performance, we only used limb and trunk variables, as these traits have been suggested to determine locomotor performance in these and other lizard species (Kaliontzopoulou et al., 2010a, 2013; Vanhooydonck and Van Damme, 2001). In the case of the association between morphology and habitat use, more than one habitat observation was available for several of the individuals sampled. To address this fact, while maximizing the use of the data available, we used the mean of each variable across observations of each individual and weighted the contribution of each individual to the pls regression by the number of habitat observations available for that individual. All statistical analyses were performed using R v. 2.14.1 (R Development Core Team, 2011).

3. Results

3.1. Morphological traits

ANOVA comparisons of morphological traits indicated that

P. bocagei and *P. g. lusitanicus* differed in total of body size, relative trunk length, relative head length and head height (Table 1, Appendix S1). ANOVA also confirmed significant differences between both sexes in SIZE and in all size-corrected traits in our sample, while some significant SP × SEX interactions were also observed. Generally, *P. bocagei* was larger in body size than *P. g. lusitanicus*, with higher but shorter heads. Males were larger in body size than females, with longer and higher heads, shorter trunks, and longer limbs.

3.2. Habitat use

The log-linear model fitted to investigate microhabitat use revealed differences in the type of substrate where each species was found (point of observation; Table 2, Fig. 1, Appendix S2), whereas no significant differences existed between sexes within each species. *P. bocagei* was found with a higher frequency on walls as compared to *P. g. lusitanicus*, which was more frequently encountered on isolated rocks (Fig. 1). ANOVA comparisons of microhabitat use indicated significant differences between species, but not between sexes, in rock diameter (Table 3). Specifically, *P. bocagei* was encountered in smaller rocks (Fig. 2) than *P. g. lusitanicus*. Linear mixed-effects models only showed significant differences between species in rock diameter ($p = 0.004$).

3.3. Locomotor performance

MANOVA comparisons on locomotor performance indicated that *P. bocagei* and *P. g. lusitanicus* differed when considering the multivariate set of maximal locomotor speeds. Univariate analyses showed that *P. bocagei* attained higher speeds in the three climbing racetracks (CLI60, CLI90 and CLI60s; Table 4, Fig. 3, Appendix S3). Sex did not have a significant effect on locomotor performance. However, post-hoc comparisons indicated that differences between both species were only significant in males and not in females (Fig. 3). ANCOVA comparisons using SIZE and weight as covariates did not reveal a significant effect of body size and/or robustness on locomotor performance (Appendix S4).

3.4. Morphology traits vs locomotor performance

Two-block partial least-squares regression did not reveal a significant association between morphological traits and locomotor performance ($r = 0.354$ and $p = 0.227$).

3.5. Morphological traits vs habitat use

Two-block partial least-squares regression indicated a significant association between both sets of variables ($r = 0.426$ and $p = 0.001$). The morphological PLS vector was most highly correlated with trunk length (positive correlation) and head height (negative correlation) (Fig. 4). The vector representing microhabitat use was most highly correlated with the percentage and the diameter of rocks, and with the percentage of vegetation, this last variable showing an opposite loading to the first two (Fig. 4). As such, the association between morphology and habitat use was summarized by multivariate vectors where lizards with longer trunks and flatter heads were more frequently found in rocks of a large diameter than in spots with vegetation.

Table 1
Results of ANOVA comparisons performed on total body size (SIZE) and size-corrected morphological traits to examine the effect of species (SP), sex and their interaction (SP*SEX). F: F-statistic, P: corresponding p-value, adjusted for multiple testing using the False Discovery Rate procedure. Significant effects are marked in bold letter. See Material and Methods for variable abbreviations.

	SP		SEX		SP*SEX	
	F	P	F	P	F	P
SIZE	17.052	**0.002**	28.706	**0.002**	4.300	**0.049**
prjTRL	19.541	**0.002**	186.958	**0.002**	8.017	**0.017**
prjHW	0.139	0.766	27.922	**0.002**	2.596	0.161
prjHH	62.798	**0.002**	9.728	**0.002**	20.875	**0.002**
prjHL	43.318	**0.002**	34.996	**0.002**	0.043	0.871
prjFLL	0.027	0.871	11.540	**0.004**	8.405	**0.013**
prjHLL	2.070	0.168	27.830	**0.002**	0.229	0.740

Table 2
Results of log-linear model performed on microhabitat use variables. See DEV: Deviance, R.DEV: Residual Deviance, P: corresponding p-value. Significant effects are marked in bold letter. Material and Methods for variable abbreviations.

	DEV	R.DEV	P
SUBS	463.122	115.123	$\mathbf{4.68 \times 10^{-100}}$
SP	76.956	38.167	$\mathbf{1.75 \times 10^{-18}}$
SEX	0.471	37.696	0.493
SUBS*SP	23.408	14.288	$\mathbf{3.32 \times 10^{-5}}$
SUBS*SEX	4.937	9.351	0.176
SP*SEX	8.837	0.514	**0.003**
SUBS*SP*SEX	0.514	0.000	0.916

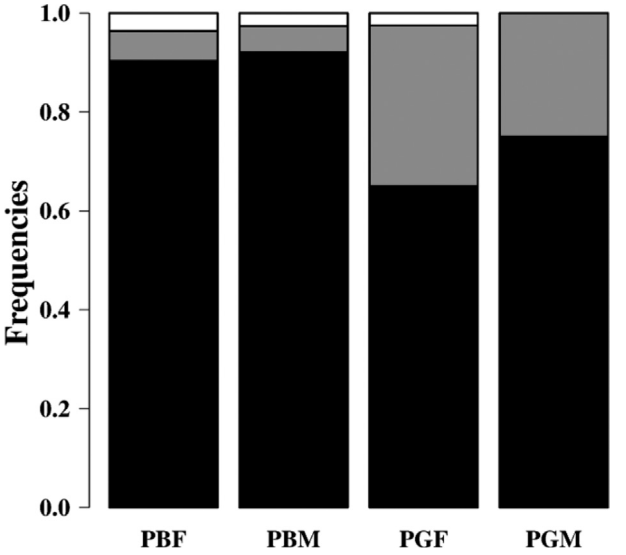

Fig. 1. Observed frequencies of each species and sex using each type of substrate. Black: walls; grey: rocks; white: others (vegetation and bare soil). PBF: *P. bocagei* females, PBM: *P. bocagei* males, PGF: *P. g. lusitanicus* females, PGM: *P. g. lusitanicus* males. See Material and Methods for variable abbreviations.

Table 3
Results of ANOVA comparisons performed on all continuously represented microhabitat (HGR, INC, ROCKD) and habitat variables (% of bare soil, vegetation and rocks) to examine the effect of species (SP), sex and their interaction (SP*SEX). F: F-statistic, P: corresponding p-value, adjusted for multiple testing using the False Discovery Rate procedure. Significant effects are marked in bold letter. See Material and Methods for variable abbreviations.

	SP		SEX		SP*SEX	
	F	P	F	P	F	P
HGR	5.783	0.086	0.803	0.687	0.097	0.818
INC	0.516	0.687	2.094	0.383	4.562	0.086
ROCKD	30.829	**0.018**	0.483	0.687	2.353	0.383
SOIL%	0.109	0.818	0.054	0.818	0.484	0.687
VEG%	6.922	0.086	0.297	0.740	0.995	0.678
ROCK%	5.947	0.086	0.386	0.687	1.760	0.459

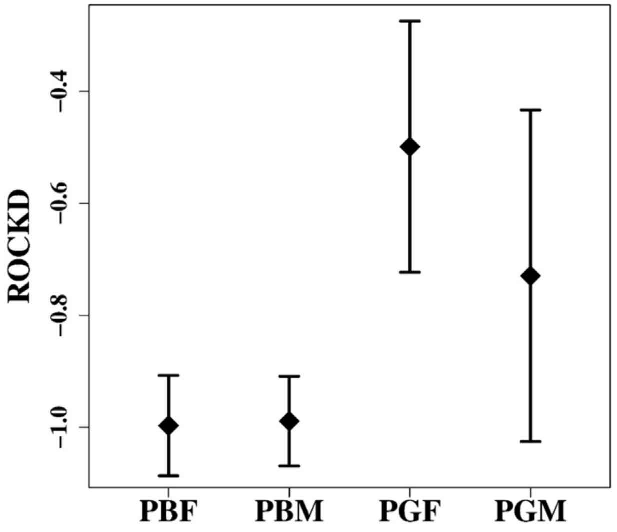

Fig. 2. Least-squares means for each species and sex for the diameter of the rock (ROCKD) at the point of observation. Vertical bars denote 95% confidence intervals. PBF: *P. bocagei* females, PBM: *P. bocagei* males, PGF: *P. g. lusitanicus* females, PGM: *P. g. lusitanicus* males. See Material and Methods for variable abbreviations.

Table 4

Results of (M)ANOVA comparisons performed on multivariate set of maximal locomotor speeds (mSPEEDS) and each type of locomotor speed separately to examine the effect of species (SP), sex and their interaction (SP*SEX). F: F-statistic, P: corresponding p-value, adjusted for multiple testing using the False Discovery Rate procedure. Significant effects are marked in bold letter. See Material and Methods for variable abbreviations.

	SP		SEX		SP*SEX	
	F	P	F	P	F	P
mSPEEDS	16.504	**0.005**	0.779	0.618	1.748	0.371
SPR	0.137	0.836	1.917	0.383	0.044	0.858
MAN	2.726	0.303	0.379	0.618	5.972	0.058
CLI60	32.446	**0.005**	1.610	0.383	2.659	0.303
CLI90	16.082	**0.005**	0.544	0.618	0.114	0.802
CLI60s	20.756	**0.005**	0.411	0.618	0.976	0.529

4. Discussion

Our investigation of the three components of the ecomorphological paradigm – morphology, locomotor performance and habitat use – in a syntopic population of *P. bocagei* and *P. g. lusitanicus* revealed an interesting pattern of ecomorphological variation, where the association between morphology and habitat is not accompanied by an association between morphology and locomotor performance. This deviates from what has been observed in numerous other lizard species (e.g. Goodman et al., 2008; Irschick et al., 2005b; Losos and Sinervo, 1989; Melville and Swain, 2000; Sinervo and Losos, 1991) and has potential implications for our understanding of the ecological and evolutionary mechanisms that underlie the high levels of morphological diversity observed in the *P. hispanica* species complex.

Although *P. bocagei* and *P. g. lusitanicus* live in strict syntopy in Moledo, our results indicate that these two forms exploit different habitat resources. Individuals of *P. g. lusitanicus* were most frequently observed on big rocks than on other substrates, while individuals of *P. bocagei* were found most frequently on human-constructed walls and rocks of a smaller diameter (Fig. 1; Fig. 2), as already suggested by others studies (Galán, 1986; Sá-Sousa et al., 2002). These results provide the first quantitative account of a significant differentiation between the two forms in terms of habitat use.

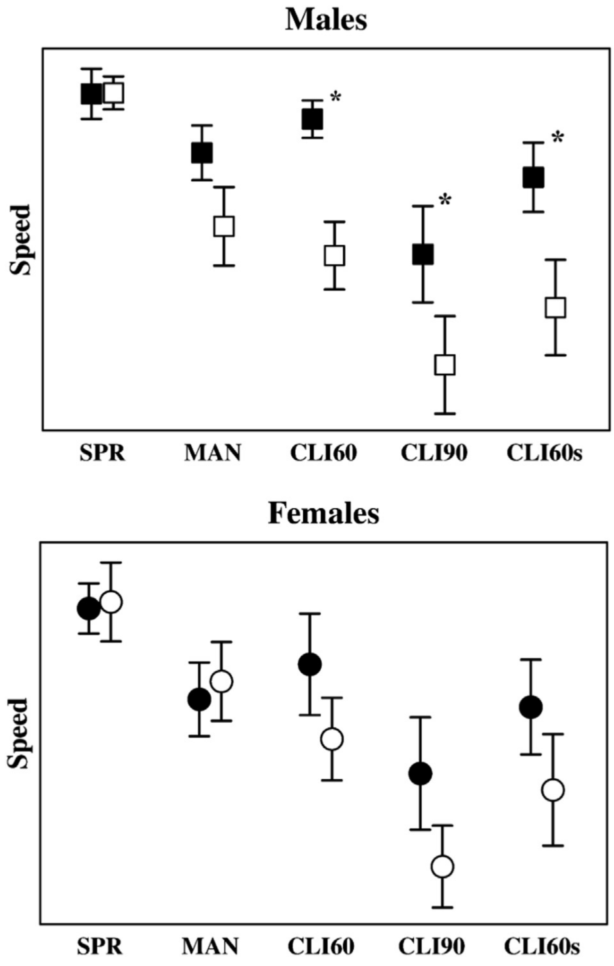

Fig. 3. Least-squares means observed in males and females of each species for the different locomotor variables quantified. Open squares, *P. g. lusitanicus*; closed squares, *P. bocagei*. Vertical bars denote 95% confidence intervals. * Significant post-hoc comparisons. See Material and Methods for variable abbreviations.

Despite this differentiation, the observed ecological differences do not correspond to the predicted differences in locomotor requirements and associated morphological traits. Instead, our results indicate that the morphological and ecological divergence between *P. bocagei* and *P. g. lusitanicus* is most probably associated to refuge use, rather than mediated by locomotor performance. Indeed, individuals of the two species from this population do not differ significantly in either limb length (Table 1), or sprinting speed (Fig. 3), but we found that *P. bocagei* climbed faster than *P. g. lusitanicus* (Fig. 3). Several factors may explain these results. First, although generally characterised as a ground-dweller, *P. bocagei* is a relatively versatile species, that uses several different types of habitats across its distribution range (Kaliontzopoulou et al., 2010a). Indeed, in the studied population it extensively uses human-constructed walls (Fig. 1). As such, this species benefits not only from enhanced sprinting, but also climbing capacities, which may explain its very good locomotor performance in the climbing racetrack (Fig. 3). Whether this pattern of locomotor differentiation between these two forms extends to other populations with different habitat availability or, instead, locomotor performance is a plastic trait in these lizards, varying across populations depending on the habitat they use, would need to be further investigated. Further, it is also important to note that, although a general

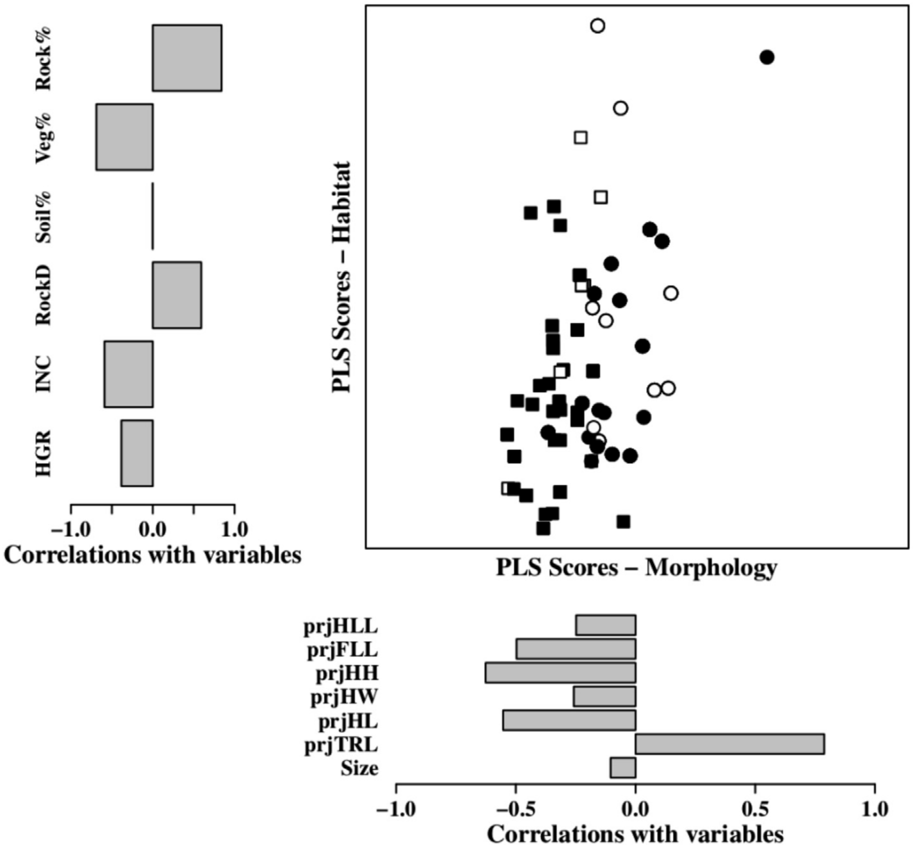

Fig. 4. Scatter-plot of individual scores of *P. bocagei* (black squares: males; black circles: females) and *P. g. lusitanicus* (white squares: males; white circles: females) obtained from partial least-squares analysis between morphological and continuous habitat variables. Bar-plots next to each axis represent the correlations observed between that axis and the variables included in each block. See Material and Methods for variable abbreviations.

association between habitat use and locomotor performance was expected based on previous studies and ecomorphological predictions, the experimental design implemented here did not allow us to directly test this association. Indeed, because of practical limitations related to the activity of the study organisms (higher activity in the spring, that also coincides with the reproductive season), here we analysed data from two different seasons (i.e. habitat use was quantified in the spring and locomotor performance in the autumn). As such, seasonality and plasticity may also have an effect on this lack of association (e.g. Irschick et al., 2006; Irschick and Meyers, 2007), although the potential role of seasonality should be investigated in detail in the future.

A high spatial and temporal plasticity of locomotor capacities may, in fact, also explain why several studies have failed to demonstrate an evolutionary link between morphology and performance in lacertids. In this study system, we could not establish a significant association between morphology and locomotor performance. Likewise, several other studies have also failed to detect similar correlations in some cases, both at the intra- and interspecific levels (Brecko et al., 2008; Goodman et al., 2008; Van Damme et al., 1997; Vanhooydonck et al., 2000), challenging the generality of the ecomorphological paradigm. Furthermore, the lack of association between morphology and locomotor performance could also be explained by other factors like behaviour (Braña, 2003; Irschick et al., 2005b; Vervust et al., 2007; Žagar et al., 2015a), physiology (e.g. muscle composition; Adolph and Pickering, 2008; Van Damme et al., 1997), biochemistry (e.g. enzyme activity; Adolph and Pickering, 2008; Van Damme et al., 1997; Vervust et al., 2007; Žagar et al., 2015b) and/or other morphological traits not investigated in this study as orientation of the limbs, differences in the claws or even the distance between the body and an inclined surface to oppose the force of gravity (Jayne and Irschick, 1999; Revell et al., 2007). In addition, the ecological and morphological segregation between the two species could be reflected in specialization in other performance traits, not examined here, such as acceleration capacity (Vanhooydonck et al., 2005), endurance (Vanhooydonck et al., 2000; Vanhooydonck, Van Damme & Aerts, 2001) and/or agility (Van Damme and Vanhooydonck, 2002). Finally, locomotor performance is involved in several ecological (feeding, thermoregulation, escape from predators, habitat and refuge use) and social (antagonistic behaviour, territory and mate acquisition, competition with heterospecifics) functions. This means that a differentiation between both species could exist when performing different tasks in nature, which may not be observable in laboratory experiments (Irschick et al., 2005a). Such a hypothesis should be further investigated in the future by examining how individuals of the two species perform in natural conditions.

The patterns observed in relation to locomotor performance do not, however, invalidate the link observed between morphology and habitat. Several studies have demonstrated a significant evolutionary correlation between morphological and environmental variation in lizards (e.g. Goodman et al., 2008; Herrel et al., 2001; Irschick et al., 2005b; Kaliontzopoulou et al., 2010a; Melville and Swain, 2000; Vanhooydonck and Van Damme, 1999; Vitt et al., 1997). The analyses conducted here, indicate a significant correlation between habitat use and morphology in a syntopic population of *P. bocagei* and *P. g. lusitanicus* in northern Portugal. Examination of variable loadings on the morphological axis obtained through two-block partial least-squares regression with habitat use reveals that trunk length and head height are the traits with the highest contributions to this association (Fig. 4). Trunk length is linked to vertebral number in *Podarcis* (Arnold, 1973), it is known to enhance body flexibility for lateral bending (Arnold, 1998; Van Damme and Vanhooydonck, 2002), and it has been associated to habitat use in lacertids (Van Damme and Vanhooydonck, 2002; Kaliontzopoulou et al., 2010b). On the other hand, habitat use has been shown to drive macroevolutionary variation in head shape, but not in body size or relative limb length in wall lizards (Kaliontzopoulou et al., 2015). As already proposed by other studies, the dorso-ventral compression of the head in rocky environments, or in saxicolous species, can derive from a mechanical constraint related to refuge use (Edwards et al., 2012; Herrel et al., 2001; Kaliontzopoulou et al., 2010a; Vanhooydonck and Van Damme, 1999; Vitt et al., 1997). Indeed, in organisms like wall lizards, which rely more on crypsis or in hiding in refuges rather than on long-distance running for predator avoidance (Carretero et al., 2006; Martín et al., 2009), habitat use may represent an evolutionary constraint for head, but not for limb traits. If this were the case here, we may expect the two species to employ different antipredatory behavioural responses. Indeed, *P. bocagei* seems to use ground-level vegetation for hiding, while *P. g. lusitanicus* usually flees towards small crevices and cracks in agricultural walls (pers. obs. of the authors). However, a detailed study of escape tactics would be necessary to test this hypothesis. Finally, the association between habitat and head traits observed here could also be driven by differences in feeding ecology between animals using different structural niches. However, this does not seem to be the case in this system, as a previous study in the same study area demonstrated that these two species do not differ in bite force or in diet (Kaliontzopoulou et al., 2012b).

Put together, the results obtained in this study reveal a significant relationship between morphological traits and habitat use in *P. bocagei* and *P. g. lusitanicus*, but, unlike what happens in numerous other lizard groups, this relationship is not accompanied by an association between morphology and locomotor performance used for fleeing. The evidence at hand does not allow us to further investigate the precise mechanisms determining this pattern and, given that this study only includes two species, we can make no extrapolations to the rest of the group (Garland and Adolph, 1994). Instead, further studies would be necessary in order to elucidate the ecological significance and plasticity of locomotor performance and habitat use in these lizards. First, understanding how maximal locomotor capacities are used in nature (e.g. for prey capture, predator avoidance, social encounters) is essential for deciphering their true evolutionary potential (Irschick et al., 2005a; Husak, 2006). Further, it would be relevant to investigate how morphological and locomotor traits are involved in shaping individual fitness (survival, mate acquisition, outcome of antagonistic encounters) in this group of lizards, and how these effects may vary across different environments.

Acknowledgements

VG was supported by a doctoral grant (SFRH/BD/93237/2013) from Fundação para a Ciência e a Tecnologia (FCT, Portugal). This research was supported by FCOMP-01-0124-FEDER-007062 FCT projects PTDC/BIA-BEC/102179/2008, PTDC/BIA-BEC/101256/2008 and PTDC/BIA-BEC/102280/2008. We are grateful to all those who assisted with field work (permit number: 67-75/2011/CAPT), Arie van der Meijden for all the help and borrowed camera to carry the lab work, and Pedro Tarroso for the help with the videos.

Appendices

Appendix S1: Descriptive statistics for the raw biometric characters in males and females of *Podarcis bocagei and P. g. lusitanicus*. Values are given as mean ± standard deviation (top) and range (bottom). See Material and Methods for variable abbreviations.

	Podarcis bocagei		*P. g. lusitanicus*	
	Males	Females	Males	Females
TRL	24.42 ± 0.68	28.58 ± 0.66	25.69 ± 0.48	26.37 ± 0.67
	17.51–32.03	18.88–34.56	22.17–32.11	18.78–33.47
HW	7.4 ± 0.21	6.52 ± 0.07	7.09 ± 0.16	5.89 ± 0.08
	5.43–9.39	5.21–7.7	5.51–8.25	4.91–6.75
HH	5.43 ± 0.13	4.63 ± 0.08	4.53 ± 0.08	3.98 ± 0.08
	3.9–6.56	3.97–5.45	3.71–5.55	3.17–4.76
FLL	16.33 ± 0.27	15.07 ± 0.31	16.21 ± 0.16	13.24 ± 0.18
	11.27–20.17	12.35–17.7	13.97–18.72	11.56–14.63
HLL	27.11 ± 0.71	24.28 ± 0.40	26.12 ± 0.44	21.45 ± 0.24
	18.68–32.8	19.44–29.98	22–30.42	18.96–23.72
HL	17.59 ± 0.48	15.65 ± 0.20	17.99 ± 0.31	14.78 ± 0.18
	12.88–21.27	12.69–17.9	14.46–19.62	12.23–16.75

Appendix S2: Descriptive statistics for the microhabitat use traits (in the point of observation) in males and females of *Podarcis bocagei* and *P. g. lusitanicus*. Values are given as mean ± standard deviation (top) and range (bottom). See Material and Methods for variable abbreviations.

	Podarcis bocagei		*P. g. lusitanicus*	
	Males	Females	Males	Females
HGR	0.83 ± 0.05	0.8 ± 0.04	0.72 ± 0.06	0.71 ± 0.05
	0–1.4	0–1.6	0.1–1.2	0–2
INC	22.72 ± 2.15	30.90 ± 2.84	34.75 ± 5.47	26.75 ± 3.58
	0–90	0–90	0–90	0–90
ROCKD	0.41 ± 0.02	0.4 ± 0.02	0.63 ± 0.13	0.79 ± 0.11
	0.1–0.9	0.1–0.9	0.25–2.5	0.2–2.5
SOIL %	4.25 ± 1.10	3.49 ± 0.9	3.50 ± 1.82	4.88 ± 2.16
	0–60	0–30	0–30	0–70
VEG%	55.48 ± 1.40	53.55 ± 1.60	47.25 ± 2.98	49.63 ± 2.72
	20–90	20–80	20–70	5–80
ROCK %	40.26 ± 1.32	42.83 ± 1.67	49.25 ± 3.21	45.00 ± 2.70
	0–80	0–80	30–80	0–95

Appendix S3: Descriptive statistics for the locomotor performance in males and females of *Podarcis bocagei* and *P. g. lusitanicus*. Values are given as mean ± standard deviation (top) and range (bottom). See Material and Methods for variable abbreviations.

	Podarcis bocagei		*P. g. lusitanicus*	
	Males	Females	Males	Females
SPR.max	118.39 ± 10.02	99.83 ± 8.53	115.82 ± 8.53	110.32 ± 13.78
	37.09–211.74	31.17–152.48	81.33–195.13	34.15–184.46
MAN.max	72.97 ± 7.26	51.06 ± 6.05	44.73 ± 6.58	60.77 ± 8.59
	33.6–110.54	13.07–89.2	12.74–107.38	18.69–105.38
CLI60.max	93.77 ± 6.09	70.49 ± 10.07	34.2 ± 4.87	40.01 ± 7.56
	38.66–131.17	12.22–123.27	15.1–71.58	16.04–98.72
CLI90.max	38.28 ± 6.3	33.72 ± 6.66	14.88 ± 2.86	14.78 ± 4.01
	8.04–87.65	5.06–84.97	3.43–37.54	5.72–60.14
CLI60s.max	64.47 ± 8.54	52.44 ± 8.28	25.37 ± 4.82	28.3 ± 7.36
	21.96–119.97	8.39–105.57	6.01–63.47	7.77–76.16

Appendix S4: Results of ANCOVA comparisons performed on multivariate set of maximal locomotor speeds (mSPEEDS) to examine the effect of species (SP), sex, their interaction (SP*SEX) and SIZE and Weight as covariate. Df: Degrees of freedom, F: F-statistic, p: corresponding p-value. Significant effects are marked in bold letter. See Material and Methods for variable abbreviations.

	Df	F	p
(Intercept)	1	1430.12	**3.01E-49**
SP	1	7.79	**2.24E-05**
SEX	1	0.51	0.77
SIZE	1	0.76	0.58
Weight	1	2.89	**0.02**
SP:SEX	1	1.18	0.33
Residuals	50		

References

Adolph, S.C., Pickering, T., 2008. Estimating maximum performance: effects of intraindividual variation. J. Exp. Biol. 211 (8), 1336–1343.

Aerts, P., Van Damme, R., Vanhooydonck, B., Zaaf, A., Herrel, A., 2000. Lizard locomotion: how morphology meets ecology. Neth. J. Zool. 50 (2), 261–277.

Amaral, M.J., Bicho, R.C., Carretero, M.A., Sanchez-Hernandez, J.C., Faustino, A.M., Soares, A.M., Mann, R.M., 2012. The use of a lacertid lizard as a model for reptile ecotoxicology studies: part 2—biomarkers of exposure and toxicity among pesticide exposed lizards. Chemosphere 87 (7), 765–774.

Arnold, E.N., 1973. Relationships of the Palaearctic Lizards Assigned to the Genera Lacerta, Algyroides and Psammodromus (Reptilia: Lacertidae). British Museum (Natural History), London.

Arnold, S.J., 1983. Morphology, performance and fitness. Am. Zool. 23 (2), 347–361.

Arnold, E.N., 1998. Structural niche, limb morphology and locomotion in lacertid lizards (Squamata, Lacertidae); a preliminary survey. Bull. Nat. Hist. Mus. Zool. Ser. 64, 63–90.

Bates, D., Maechler, M., Bolker, B., Walker, S., Christensen R,Singmann H,Dai, B., 2014. lme4: Linear Mixed-effects Models Using Eigen and S4. R package version 1.1-7.

Bauwens, D., Thoen, C., 1981. Escape tactics and vulnerability to predation associated with reproduction in the lizard *Lacerta vivipara*. J. Anim. Ecol. 50 (3), 733–743.

Braña, F., 2003. Morphological correlates of burst speed and field movement patterns: the behavioural adjustment of locomotion in wall lizards (*Podarcis muralis*). Biol. J. Linn. Soc. 80 (1), 135–146.

Brecko, J., Huyghe, K., Vanhooydonck, B., Herrel, A., Grbac, I., Van Damme, R., 2008. Functional and ecological relevance of intraspecific variation in body size and shape in the lizard *Podarcis melisellensis* (Lacertidae). Biol. J. Linn. Soc. 94 (2), 251–264.

Carretero, M.A., Vasconcelos, R., Fonseca, M., Kaliontzopoulou, A., Brito, J.C., Harris, D.J., Perera, A., 2006. Escape tactics of two syntopic forms of the *Lacerta perspicillata* complex with different colour patterns. Can. J. Zool. 84 (11), 1594–1603.

Carretero, M.A., 2008. An integrated assessment of a group with complex systematics: the Iberomaghrebian lizard genus Podarcis (Squamata, Lacertidae). Integr. Zool. 3 (4), 247–266.

Carretero, M.A., García-Muñoz, E., Kaliontopoulou, A., Gomes, V., Carneiro, D., Žagar, A., Sillero, N., 2012. Evolutionary ecophysiology of lacertid lizards. In: Do Preferred Temperatures and Water Loss Rates Trade-off in Podarcis? 7th World Congress of Herpetology, Vancouver (Canada), pp. 8–14. August 2012.

Clemente, C.J., Withers, P.C., Thompson, G.G., Lloyd, D., 2013. Lizard tricks: overcoming conflicting requirements of speed versus climbing ability by altering biomechanics of the lizard stride. J. Exp. Biol. 216 (20), 3854–3862.

Collar, D.C., Schulte, J.A., O'meara, B.C., Losos, J.B., 2010. Habitat use affects morphological diversification in dragon lizards. J. Evol. Biol. 23 (5), 1033–1049.

Da Silva, J.M., Herrel, A., Measey, G.J., Vanhooydonck, B., Tolley, K.A., 2014. Linking microhabitat structure, morphology and locomotor performance traits in a recent radiation of dwarf chameleons (Bradypodion). Funct. Ecol. http://dx.doi.org/10.1111/1365-2435.12210.

Domínguez, J.F., Salvador, A., 1989. Selección de microhábitat en *Lacerta schreiberi* Bedriaga, 1878 y *Podarcis bocagei* (Seoane, 1884) en una localidad de la Cordillera Cantábrica, España (Reptilia, Lacertidae). Bol. Real Soc. Española Hist. Nat. Secc. Biol. 84, 273–286.

Edwards, S., Vanhooydonck, B., Herrel, A., Measey, G.J., Tolley, K.A., 2012. Convergent evolution associated with habitat decouples phenotype from phylogeny in a clade of lizards. PLoS One 7 (12), e51636.

Elstrott, J., Irschick, D.J., 2004. Evolutionary correlations among morphology, habitat use and clinging performance in Caribbean Anolis lizards. Biol. J. Linn. Soc. 83 (3), 389–398.

Galán, P., 1986. Morfología y distribución del género Podarcis Wagler, 1830 (Sauria, Lacertidae) en el noroeste de la Península Ibérica. Rev. Española Herpetol. 1, 85–142.

Galán, P., 1994. Selección del microhábitat en una población de *Podarcis bocagei* del noroeste ibérico. Doñana Acta Vertebr. 21 (2), 153–168.

García-Muñoz, E., Sillero, N., 2010. Two new types of noose for capturing herps. Acta Herpetol. 5 (2), 259–263.

Garland Jr., T., Adolph, S.C., 1994. Why not to do two-species comparative studies: limitations on inferring adaptation. Physiol. Zool. 67 (4), 797–828.

Garland Jr., T., Losos, J.B., 1994. Ecological morphology of locomotor performance in squamate reptiles. In: Wainwright, P.C., Reilly, S.M. (Eds.), Ecological Morphology: Integrative Organismal Biology. University of Chicago Press, Chicago, pp. 240–302.

Geniez, P., Sá-Sousa, P., Guillaume, C.P., Cluchier, A., Crochet, P.A., 2014. Systematics of the *Podarcis hispanicus* complex (Sauria, Lacertidae) III: valid nomina of the western and central Iberian forms. Zootaxa 3794 (1), 1–51.

Goodman, B.A., 2007. Divergent morphologies, performance, and escape behaviour in two tropical rock-using lizards (Reptilia: Scincidae). Biol. J. Linn. Soc. 91 (1), 85–98.

Goodman, B.A., Miles, D.B., Schwarzkopf, L., 2008. Life on the rocks: habitat use drives morphological and performance evolution in lizards. Ecology 89 (12), 3462–3471.

Gosá, A., Jover, L., Bea, A., 1986. Contribución a la taxonomía de *Podarcis muralis* (Laurenti, 1768) y *Podarcis hispanica* Steindachner, 1870 en la Península Ibérica (País Vasco y Sistema Central). Munibe 38, 109–120.

Herrel, A., Meyers, J.J., Vanhooydonck, B., 2001. Correlations between habitat use and body shape in a phrynosomatid lizard (*Urosaurus ornatus*): a population-level analysis. Biol. J. Linn. Soc. 74 (3), 305–314.

Husak, J.F., 2006. Does survival depend on how fast you can run or how fast you do run? Funct. Ecol. 20 (6), 1080–1086.

Irschick, D.J., Garland Jr., T., 2001. Integrating function and ecology in studies of adaptation: investigations of locomotor capacity as a model system. Annu. Rev. Ecol. Syst. 32 (1), 367–396.

Irschick, D.J., 2002. Evolutionary approaches for studying functional morphology: examples from studies of performance capacity. Integr. Comp. Biol. 42 (2), 278–290.

Irschick, D.J., Herrel, A., Vanhooydonck, B., Huyghe, K., Van Damme, R., 2005a. Locomotor compensation creates a mismatch between laboratory and field estimates of escape speed in lizards: a cautionary tale for performance-to-fitness studies. Evolution 59 (7), 1579–1587.

Irschick, D.J., Carlisle, E., Elstrott, J., Ramos, M., Buckley, C., Vanhooydonck, B., Meyers, J., Herrel, A., 2005b. A comparison of habitat use, morphology, clinging performance and escape behaviour among two divergent green anole lizard (*Anolis carolinensis*) populations. J. Linn. Soc. 85 (2), 223–234.

Irschick, D.J., Ramos, M., Buckley, C., Elstrott, J., Carlisle, E., Lailvaux, S., Bloch, N., Herrel, A., VanHooydonck, B., 2006. Are morphology-performance relationships invariant across different seasons? a test with the green anole lizard (*Anolis carolinensis*). Oikos 114 (1), 49–59.

Irschick, D.J., Meyers, J.J., 2007. An analysis of the relative roles of plasticity and natural selection on morphology and performance in a lizard (*Urosaurus ornatus*). Oecologia 153 (2), 489–499.

Irschick, D.J., Meyers, J.J., Husak, J.F., Le Galliard, J.F., 2008. How does selection operate on whole-organism functional performance capacities? a review and synthesis. Evol. Ecol. Res. 10 (2), 177–196.

Jayne, B.C., Irschick, D.J., 1999. Effects of incline and speed on the three-dimensional hindlimb kinematics of a generalized iguanian lizard (*Dipsosaurus dorsalis*). J. Exp. Biol. 202 (2), 143–159.

Kaliontzopoulou, A., Carretero, M.A., Llorente, G.A., 2007. Multivariate and geometric morphometrics in the analysis of sexual dimorphism variation in Podarcis lizards. J. Morphol. 268 (2), 152–165.

Kaliontzopoulou, A., Carretero, M.A., Llorente, G.A., 2010a. Intraspecific ecomorphological variation: linear and geometric morphometrics reveal habitat-related patterns within *Podarcis bocagei* wall lizards. J. Evol. Biol. 23 (6), 1234–1244.

Kaliontzopoulou, A., Carretero, M.A., Llorente, G.A., 2010b. Sexual dimorphism in traits related to locomotion: ontogenetic patterns of variation in Podarcis wall lizards. Biol. J. Linn. Soc. 99 (3), 530–543.

Kaliontzopoulou, A., Pinho, C., Harris, D.J., Carretero, M.A., 2011. When cryptic diversity blurs the picture: a cautionary tale from Iberian and North African Podarcis wall lizards. Biol. J. Linn. Soc. 103 (4), 779–800.

Kaliontzopoulou, A., Carretero, M.A., Llorente, G.A., 2012a. Morphology of the Podarcis wall lizards (Squamata: Lacertidae) from the Iberian Peninsula and North Africa: patterns of variation in a putative cryptic species complex. Zool. J. Linn. Soc. 164 (1), 173–193.

Kaliontzopoulou, A., Adams, D.C., van der Meijden, A., Perera, A., Carretero, M.A., 2012b. Relationships between head morphology, bite performance and ecology in two species of Podarcis wall lizards. Evol. Ecol. 26 (4), 825–845.

Kaliontzopoulou, A., Bandeira, V., Carretero, M.A., 2013. Sexual dimorphism in locomotor performance and its relation to morphology in wall lizards (*Podarcis bocagei*). J. Zool. 289 (4), 294–302.

Kaliontzopoulou, A., Carretero, M.A., Adams, D.C., 2015. Ecomorphological variation in male and female wall lizards and the macroevolution of sexual dimorphism in relation to habitat use. J. Evol. Biol. http://dx.doi.org/10.1111/jeb.12540.

Losos, J.B., Sinervo, B., 1989. The effects of morphology and perch diameter on sprint performance of Anolis lizards. J. Exp. Biol. 145 (1), 23–30.

Martín, J., Luque-Larena, J.J., Lopez, P., 2009. When to run from an ambush predator: balancing crypsis benefits with costs of fleeing in lizards. Anim. Behav. 78 (4), 1011–1018.

Melville, J., Swain, R., 2000. Evolutionary relationships between morphology, performance and habitat openness in the lizard genus Niveoscincus (Scincidae: Lygosominae). Biol. J. Linn. Soc. 70 (4), 667–683.

Mevik, B.H., Wehrens, R., Liland, K.H., 2011. pls: Partial Least Squares and Principal Component Regression. R package version 2.3-0.

Miles, D.B., 2004. The race goes to the swift: fitness consequences of variation in sprint performance in juvenile lizards. Evol. Ecol. Res. 6 (1), 63–75.

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Wagner, H., 2012. vegan: Community Ecology Package. R package version 2.0–3.

Pérez Mellado, V., 1980. La lagartija de Bocage, *Podarcis bocagei* (SEOANE, 1884): primeros datos sobre su distribución, colorido y ecología. Amphib. Reptil. 3–4, 253–268.

R Core Team, 2011. R: a language and environment for statistical computing. Vienna, Austria R Foundation for Statistical Computing. URL. http://www.R-project.org/.

Revell, L.J., Johnson, M.A., Schulte, J.A., Kolbe, J.J., Losos, J.B., 2007. A phylogenetic test for adaptive convergence in rock-dwelling lizards. Evolution 61 (12), 2898–2912.

Ricklefs, R.E., Cochran, D., Pianka, E.R., 1981. A morphological analysis of the structure of communities of lizards in desert habitats. Ecology 62 (6), 1474–1483.

Sá-Sousa, P., 2001. A Controversa Sistemática das Lagartixas do género Podarcis Wagler 1830 (Sauria: Lacertidae) em Portugal (PhD Thesis). University of Lisboa, Lisbon.

Sá-Sousa, P., Vicente, L., Crespo, E.G., 2002. Morphological variability of *Podarcis hispanica* (Sauria: Lacertidae) in Portugal. Amphib. Reptil. 23 (1), 55–70.

Sinervo, B., Losos, J.B., 1991. Walking the tight rope: arboreal sprint performance among *Sceloporus occidentalis* lizard populations. Ecology 72 (4), 1225–1233.

Tsuji, J.S., Huey, R.B., van Berkum, F.H., Garland Jr., T., Shaw, R.G., 1989. Locomotor performance of hatchling fence lizards (*Sceloporus occidentalis*): quantitative genetics and morphometric correlates. Evol. Ecol. 3 (3), 240–252.

Van Berkum, F.H., Tsuji, J.S., 1987. Inter-familial differences in sprint speed of hatchling *Sceloporus occidentalis*. J. Zool. 212 (3), 511–519.

Van Berkum, F.H., Huey, R.B., Tsuji, J.S., Garland, T., 1989. Repeatability of individual differences in locomotor performance and body size during early ontogeny of the lizard Sceloporus occidentalis (Baird & Girard). Funct. Ecol. 3 (1), 97–105.

Van Damme, R., Aerts, P., Vanhooydonck, B., 1997. No trade-off between sprinting and climbing in two populations of the Lizard *Podarcis hispanica* (Reptilia: Lacertidae). Biol. J. Linn. Soc. 60 (4), 493–503.

Van Damme, R., Vanhooydonck, B., 2002. Speed versus manoeuvrability: association between vertebral number and habitat structure in lacertid lizards. J. Zool. 258 (3), 327–334.

Vanhooydonck, B., Van Damme, R., 1999. Evolutionary relationships between body shape and habitat use in lacertid lizards. Evol. Ecol. Res. 1 (7), 785–805.

Vanhooydonck, B., Van Damme, R., Aerts, P., 2000. Ecomorphological correlates of habitat partitioning in Corsican lacertid lizards. Funct. Ecol. 14 (3), 358–368.

Vanhooydonck, B., Van Damme, R., 2001. Evolutionary trade-offs in locomotor capacities in lacertid lizards: are splendid sprinters clumsy climbers? J. Evol. Biol. 14 (1), 46–54.

Vanhooydonck, B., Van Damme, R., Aerts, P., 2001. Speed and stamina trade-off in lacertid lizards. Evolution 55, 1040–1048.

Vanhooydonck, B., Andronescu, A., Herrel, A., Irschick, D.J., 2005. Effects of substrate structure on speed and acceleration capacity in climbing geckos. Biol. J. Linn. Soc. 85 (3), 385–393.

Vervust, B., Grbac, I., Van Damme, R., 2007. Differences in morphology, performance and behaviour between recently diverged populations of *Podarcis sicula* mirror differences in predation pressure. Oikos 116 (8), 1343–1352.

Vitt, L.J., Caldwell, J.P., Zani, P.A., Titus, T.A., 1997. The role of habitat shift in the evolution of lizard morphology: evidence from tropical Tropidurus. Proc. Natl. Acad. Sci. 94 (8), 3828–3832.

Žagar, A., Carretero, M.A., Osojnik, N., Sillero, N., Vrezec, A., 2015a. A place in the sun: does interspecific interference affect thermoregulation in coexisting lizards? Behav. Ecol. Sociobiol. 69, 1127–1137.

Žagar, A., Simčič, T., Carretero, M.A., Vrezec, A., 2015b. The role of metabolism in understanding altitudinal segregations: a case of two potentially interacting lizards. Comp. Biochem. Physiol. A 179, 1–6.