Journal of Zoology. Print ISSN 0952-8369

Sexual dimorphism in locomotor performance and its relation to morphology in wall lizards (*Podarcis bocagei*)

A. Kaliontzopoulou[1,2], V. Bandeira[3] & M. A. Carretero[1]

1 CIBIO/UP, Centro de Investigação em Biodiversidade e Recursos Genéticos, Universidade do Porto, Vairão, Portugal
2 Department of Ecology, Evolution, and Organismal Biology, Iowa State University, Ames, IA, USA
3 Departamento de Biologia and CESAM, Universidade de Aveiro, Aveiro, Portugal

Keywords
sexual dimorphism; morphology; locomotion; sexual selection; territory defence

Correspondence
Antigoni Kaliontzopoulou, CIBIO/UP Centro de Investigação em Biodiversidade e Recursos Genéticos, Vairão, Portugal.
Email: antigoni@cibio.up.pt

Editor: Andrew Kitchener

Received 26 March 2012; revised 11 September 2012; accepted 16 November 2012

doi:10.1111/jzo.12006

Abstract

Sexual dimorphism (SD) is the result of evolutionary pressures acting differentially on members of each sex. Investigating the association between SD observed in different sets of phenotypic traits, which are evolutionarily linked, can shed light on the mechanisms causing SD variation within and across species. Although the association between morphology and locomotor performance is a major paradigm in ecomorphology, substantially less effort has been dedicated to investigate the covariation between both sets of traits in the context of sexual divergence. Here, we investigated morphology and locomotor performance in wall lizards *Podarcis bocagei* to determine if locomotor SD exists in this species, as one may expect based on the morphological SD observed, and test whether both types of SD are directly associated. Our results indicate that significant morphological and locomotor SD exists in this species, reporting a significant locomotor SD for the first time in this genus of lizards. Our study also provides evidence that a direct association between morphology and performance exists at the individual level, binding together SD in both sets of traits. The observed patterns of SD suggest that male locomotor capacity and the corresponding morphological features are well suited for sprinting in level surfaces, but less so for other types of locomotion, potentially as a result of sexual selection acting on male locomotor performance through influences on territory defence and reproductive fitness.

Introduction

Sexual dimorphism (SD), the phenotypic difference between males and females of a species, is a major paradigm in evolutionary biology. Comprehending the circumstances under which sexually divergent phenotypes are produced from a largely shared gene pool requires understanding of both the proximate and evolutionary mechanisms involved. From an evolutionary perspective, SD results from the combined influence of numerous forces, which act differentially on each sex-modifying phenotypic components that influence their capacity of fulfilling their ecological and social roles (Andersson, 1994; Fairbairn, 1997). In this context, morphological SD, which encompasses both size and shape, may be the outcome of selection on one or several performance and/or life-history traits. For instance, male-biased SD in total body size and the relative size of structures involved in antagonistic behaviour is commonly explained by the dominance advantages gained by larger males in relation to territorial behaviour and access to mates (Stamps, 1983; Huyghe *et al*., 2005; Lailvaux & Irschick, 2007*a*; Lindenfors, Gittleman & Jones, 2007). In such cases, sexual selection modifies morphological features by favouring different whole-organism performance optima (Lailvaux & Irschick, 2006). As such, understanding how morphological and functional SD are interrelated can shed light on the precise mechanisms involved in SD evolution within and across taxa.

Locomotor performance is essential for both escape from predators and prey capture, and can thus be under strong selective pressures (Van Damme *et al*., 2003; Husak, 2006). The association between morphology and locomotor performance in lizards has been a topic of intense study for years. Locomotion has been shown to provide the critical link between morphological variation and habitat use in many lizard groups, thus constituting a textbook example in ecomorphology and adaptive radiation (Garland & Losos, 1994; Aerts *et al*., 2000; Irschick & Garland, 2001). Notably, the relationship between SD in morphology and locomotor performance has received less attention (Lailvaux, 2007). This is surprising, as territory defence, agonistic interactions and mate acquisition are essential components of sexual selection in many lizard species, and locomotor performance has been shown to directly enhance antagonistic capacity and increase reproductive fitness in males (Huyghe *et al*., 2005; Husak *et al*., 2006; Husak & Fox, 2008; Husak, Fox & Van Den Bussche, 2008), thus providing a potential link between SD in morphology and locomotion. Indeed, territoriality is frequently invoked to explain size SD in lizards (Stamps, 1983).

The studies that have investigated locomotor SD in lizards have given variable results (reviewed by Lailvaux, 2007). In some cases, no sexual differences have been detected in any of the studied traits (Cullum, 1998; Brecko *et al*., 2008; Iraeta *et al*., 2011). In others, some traits differ in absolute value between both sexes, but such differences are fully explained by size SD (Snell *et al*., 1988; Miles, Snell & Snell, 2001; Braña, 2003). Yet, in others, locomotor SD persists even after correction for body size effects (Lailvaux, Alexander & Whiting, 2003; Lailvaux & Irschick, 2007*b*). Interestingly, SD in lizard body shape often encompasses morphological traits that have been associated with locomotor performance (Kaliontzopoulou, Carretero & Llorente, 2010*a*), at least in an ecomorphological context. Indeed, male lizards frequently show longer limbs and shorter trunks than females, a morphological pattern that could be reflected in the locomotion of both sexes. Relatively longer limbs may enhance running in flat surfaces, while a longer trunk could enhance manoeuvrability, as predicted by biomechanical models and suggested by interspecific studies in lizards (Van Damme *et al*., 2003), thus explaining locomotor SD. However, sexual differences in other traits, such as physiology or behaviour, may also influence SD in locomotor performance (Husak & Fox, 2008). As such, investigating the association between locomotor and morphological SD can provide insights to the mechanisms involved in SD evolution. Specifically, a significant association between morphological and locomotor SD would provide empirical evidence to the correlated evolution of both phenotypic traits and could point to selection acting in conjunction on form and function.

Here, we investigate morphological and locomotor SD in *Podarcis bocagei* (Seoane, 1884), a lacertid lizard endemic to the north-west Iberian Peninsula, to test whether locomotor capacities vary between both sexes in this lizard species, a pattern that would suggest different evolutionary forces acting on performance of males and females. Further, we tested the hypothesis that variation in locomotor performance among individuals is related to morphological traits, as suggested by biomechanical observations on other lizard species. Finally, we examined whether SD in morphology and performance interrelated, a pattern that might suggest the coevolution of both types of SD, under selective mechanisms that influence performance through morphological modifications.

Materials and methods

A total of 12 adult male and 12 adult female *P. bocagei* were collected in São Mamede do Coronado (North-West Portugal) during September 2008. We avoided studying locomotion during the reproductive season, as gravidity influences female locomotor performance (Van Damme, Bauwens & Verheyen, 1989; Schwarzkopf & Shine, 1992). All lizards were collected from granitic agricultural walls, which are the predominant habitat they use in this locality (Kaliontzopoulou, Carretero & Llorente, 2010*b*). We examined only adult lizards, considering as adults all individuals larger than 45 mm in snout – vent length (SVL) (Carretero *et al*., 2006). Immediately after capture, all lizards were transported to the laboratory where they were kept in individual terraria, under natural light conditions and with food and water supplied *ad libitum*. After the end of the experiments, all individuals were released back to the site where they were captured.

Morphological traits and variables

To quantify morphology potentially associated with locomotion (Kaliontzopoulou *et al*., 2010*a*), we measured the following linear biometric traits to the closest 0.01 mm using electronic callipers: trunk length (TRL), fore limb length (FLL), hind foot length including the fourth toe (4TL) and total hind limb length (HLL). In order to separate size and shape effects, we first calculated the isometric size (SIZE) of each individual by projecting all log-transformed linear measurements on an isometric vector (Kaliontzopoulou *et al*., 2010*b*). We then regressed each linear trait on SIZE and retained the regression residuals (hereof prjTRL, prjFLL, prj4TL and prjHLL), which were used as size-corrected variables to represent shape variation (Kaliontzopoulou *et al*., 2010*b*). As such, hereafter we refer to the combined multivariate matrix of all size-corrected variables as 'SHAPE', when multivariate analyses are involved, and to each projected variable by its denomination as given earlier, when univariate analyses were conducted.

Locomotor performance

Two days of rest were allowed between the arrival to the laboratory and the beginning of locomotor experiments to ensure acclimatization. Performance experiments were carried out under controlled temperature of about 31°C. Although selected body temperatures are generally thought to be evolutionarily fixed within a species (i.e. Van Damme, Bauwens & Verheyen, 1990), some variation may still exist among populations or individuals of the same species. As such, we conducted our experiments under thermal conditions that approximated the selected body temperature of this species measured in our study area (Amaral *et al*., 2012). Before the experiments, the lizards were allowed to thermoregulate in individual terraria, exposed to direct natural light for about an hour, to ensure activity body temperatures.

Because *P. bocagei* is quite flexible in terms of habitat use, generally being a ground-dwelling lizard but also exploiting agricultural walls and vegetation (Kaliontzopoulou *et al*., 2010*b*; Galán, 2011), we examined locomotor performance under different experimental settings to quantify different speed components (Vanhooydonck & Van Damme, 2001, 2003). Sprinting speed was measured in a 1.7-m long and 15-cm wide racetrack with cork substrate. Climbing and clambering speed were measured in a 1-m long and 15-cm wide racetrack, tilted to an angle of 65° and with cork and wire mesh substrates, respectively. Manoeuvrability was measured as the speed of running through a pinboard, made of 8-mm diameter pins placed at equal distances of 35 mm, following previous studies on the manoeuvrability of *Podarcis*

(Vanhooydonck & Van Damme, 2003). All trials were filmed with a digital camera (Canon XM-2 camcorder, Amstelveen, The Netherlands) at a filming speed of 25 fps. All animals were tested five times in each setting, to ensure that maximal performance capacity was recorded (Losos, Creer & Schulte, 2002; Adolph & Pickering, 2008). Trials of each individual were randomized to ensure that all lizards were tested during different days and hours and avoid sequential repeats of the same trial. A rest of at least 2 hours between trials was allowed to ensure physical recovery of the individuals. The quality of each trial was examined prior to analyses, and ‘poor’ trials (*sensu* Van Berkum & Tsuji, 1987; Tsuji *et al*., 1989) were eliminated.

The position of the lizard across each trial was digitized using MaxTRAQ 2D motion analysis software (Innovision Systems Inc., 2009). Maximum instantaneous speed across each trial was calculated using MaxMATE motion tool-kit (Innovision Systems Inc., 2007). Because most studies available quantify running speed across distance intervals, instead of examining instantaneous speed, we also examined maximum speed across any 10-cm interval, and all analyses were conducted examining two sets of speed data: instantaneous and across 10-cm intervals. The maximum speed per individual across trials (considering either instantaneous or 10-cm interval speeds) was retained for statistical analyses. All speed variables were log-transformed prior to analyses.

Statistical procedures

To test for SD, we examined the effect of SEX on morphology and locomotor performance through multivariate analysis of variance (MANOVA). All morphological variables fulfilled the assumptions of normality (Shapiro – Wilk’s test, $P > 0.05$ in all cases) and homogeneity of variances (Bartlett’s test, $P > 0.05$ in all cases). We performed MANOVA on body shape and univariate ANOVAs for each of body size and size-corrected body parts. To test for the existence of SD in locomotion traits, we performed a MANOVA and a repeated-measures ANOVA on the instantaneous and 10-cm interval speed datasets, with SEX as a between-subjects factor and the type of locomotion test as a within-subject factor. Before repeated-measures ANOVA, deviations from sphericity were examined using Mauchly’s test. The instantaneous-speeds dataset did not significantly deviate from sphericity ($W = 0.82$; $P = 0.52$), but the 10-cm interval one did ($W = 0.48$; $P = 0.01$). To account for this fact, ANOVA P-values were corrected using the Greenhouse – Geisser correction (Maxwell & Delaney, 1990). When significant effects were observed, pairwise differences between groups (within sexes, across experiments and across sexes, within experiments) were examined using planned comparisons. Repeated-measures ANOVA designs were conducted using the R-package *ez* (Lawrence, 2012) and planned comparisons were conducted using the R-package *multcomp* (Hothorn, Bretz & Westfall, 2008).

To test whether SIZE or SHAPE could explain the observed SD in locomotor performance, we performed multivariate analysis of covariance (MANCOVA) comparisons with the multivariate set of measured speeds as the response, SEX as the categorical predictor and SIZE or SHAPE as covariates. Finally, to visualize the relationship between morphology and locomotor performance in a multivariate framework, we performed a canonical correlation analysis (Legendre & Legendre, 1998) using the R-package *vegan* (Oksanen *et al*., 2012). To test the significance of the observed correlation between canonical vectors, we followed a permutation procedure with 1000 permutations (Rohlf & Corti, 2000). All statistical analyses were performed using R v. 2.14.2 (R Development Core Team, 2012).

Results

MANOVA comparisons indicated that both sexes differed in body size and shape (Table 1). Males of *P. bocagei* were larger than females in total body size, with relatively longer fore and hind limbs, but relatively shorter trunks (Fig. 1, Table 2). MANOVA on speed variables indicated significant differences between both sexes, both when considering instantaneous and 10-cm interval speeds (Table 1). This was due to a difference between sexes in speed variation across locomotor conditions, as indicated by a significant interaction between locomotion type and SEX in the repeated-measures ANOVAs (Table 1). In fact, planned comparisons within sexes indicated that locomotion speeds were uniform across conditions for females ($P > 0.1$ in all cases), but males showed significantly higher sprinting speeds as compared with climbing and clambering speeds and manoeuvrability ($P < 0.05$ for all comparisons, Fig. 2, Table 2). MANCOVA comparisons on the multivariate set of locomotion speeds indicated that sexes still differed in locomotor performance when accounting for body size or body shape, at least when considering instantaneous speeds (Table 3).

The examination of the relationship between morphology and locomotion in a multivariate framework using canonical correlation analysis yielded a single significant canonical correlation dimension of association between both variable blocks in the case of instantaneous speeds ($r = 0.811$, $P = 0.024$), but not when using 10-cm interval speeds as the Y block ($r = 0.735$, $P = 0.081$). Considering the analysis involving instantaneous speeds, the morphological canonical vector of association was most highly correlated with body size and hind limb length (Fig. 3). The corresponding locomotion vector was most highly correlated with sprint speed, but also clambering speed and manoeuvrability, where clambering speed exhibited an opposite-sign correlation with the vector as compared with the remaining variables (Fig. 3). Both sexes were visibly segregated across the multivariate space defined by morphological and locomotion canonical correlation axes (Fig. 3).

Discussion

Understanding the associations between SD observed in different phenotypic traits is essential for our comprehension of SD evolution. Our study indicates a significant intraspecific association between morphology and locomotor performance, which binds together sexual variation in both sets of

Table 1 Results of MANOVA comparisons performed on morphological and locomotor performance traits to examine between-sex differences

		Morphology			
		SS/Pillai	*F*	d.f.	*P*
Isometric size		0.013	17.098	1, 22	**4.34×10^{-4}**
Multivariate shape		0.412	4.670	1, 22	**0.013**
prjTRL		0.014	8.813	1, 22	**0.007**
prjFLL		0.003	11.640	1, 22	**0.003**
prj4TL		3.73×10^{-4}	0.405	1, 22	0.531
prjHLL		0.002	5.178	1, 22	**0.033**
		Locomotion – multivariate			
		Pillai	*F*	d.f.	*P*
Instantaneous speeds		0.502	4.781	4, 19	**0.008**
10-cm interval speeds		0.383	2.952	4, 19	**0.047**
		Locomotion – repeated measures			
		ES	*F*	d.f.	*P*
Instantaneous speeds	SEX	$2.48*10^{-4}$	0.009	1, 22	0.927
	Loc. type	0.160	11.642	3, 66	**3.24×10^{-6}**
	SEX × loc. type	0.079	5.252	3, 66	**0.003**
10-cm interval speeds	SEX	$1.47*10^{-4}$	0.005	1, 22	0.943
	Loc. type	0.183	12.887	3, 66	**4.15×10^{-5}** [a]
	SEX × loc. type	0.054	3.322	3, 66	**0.045**[a]

[a]Due to deviation from the assumption of sphericity, these *P*-values have been corrected using the Greenhouse–Geisser correction (Maxwell & Delaney, 1990). *P*-values significant at the 0.05 level are in bold. See Materials and methods section for abbreviations of variables. SS, sums of squares for ANOVA; Pillai, Pillai' s trace for MANOVA; *F*, exact or approximate *F*-value (for ANOVA and MANOVA, correspondingly); *P*, corresponding *P*-value; d.f., degrees of freedom (effects, residuals); ES, effect size for repeated-measures ANOVA effects; ANOVA, analysis of variance; MANOVA, multivariate analysis of variance.

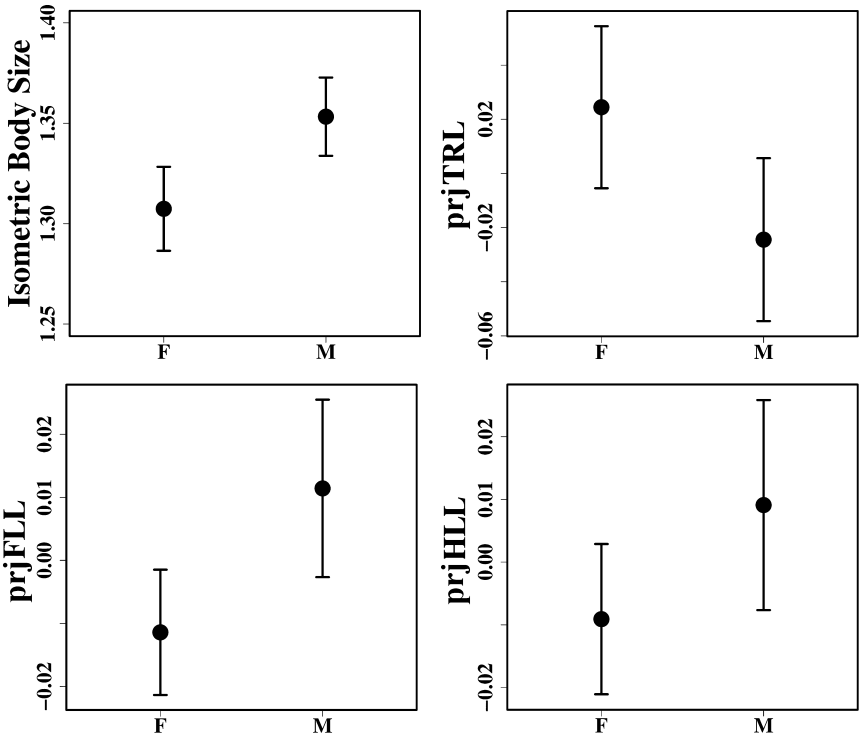

Figure 1 Least-squares means observed in each sex for those morphological variables that showed significant sexual variation (Table 1), including total body size obtained by isometric projection and size-corrected length of the trunk (prjTRL), the fore (prjFLL) and the hind limb (prjHLL). F, females; M, males. Vertical bars denote 95% confidence intervals.

Table 2 Descriptive statistics for the morphological traits, instantaneous and 10-cm interval locomotor speeds examined in this study, for males and females of *Podarcis bocagei*

	Males (n = 12)	Females (n = 12)
Morphology		
Trunk length (mm)	30.24 ± 0.96	31.76 ± 1.08
	(23.87–35.6)	(25.07–37.71)
Fore limb length (mm)	21.09 ± 0.29	17.71 ± 0.32
	(18.72–22.39)	(16.07–19.85)
Hind foot length (mm)	14.04 ± 0.39	12.3 ± 0.28
	(11.07–16.02)	(11.24–14.78)
Hind limb length (mm)	29.29 ± 0.61	24.81 ± 0.39
	(24.32–31.7)	(22.12–26.72)
Instantaneous speeds		
Sprint speed (cm sec^{-1})	161.21 ± 9.28	139.56 ± 10.15
	(119.33–211.86)	(95.97–207.1)
Climbing speed (cm sec^{-1})	125.05 ± 8.41	132.07 ± 7.15
	(70.71–170.45)	(82.76–165.79)
Clambering speed (cm sec^{-1})	111.52 ± 5.12	129.55 ± 7.3
	(86.47–131.11)	(93.21–171.4)
Manoeuvrability (cm sec^{-1})	124.09 ± 4.59	121.02 ± 5.82
	(106.87–162.96)	(91.59–160.69)
10-cm interval speeds		
Sprint speed (cm sec^{-1})	157.88 ± 11.98	138.97 ± 12.9
	(100.52–241.52)	(82.09–243.43)
Climbing speed (cm sec^{-1})	113.86 ± 11.78	124.57 ± 8.09
	(33.67–170.45)	(69.75–159.79)
Clambering speed (cm sec^{-1})	103.97 ± 6.3	123.46 ± 9.76
	(67.62–131.11)	(71.81–201.11)
Manoeuvrability (cm sec^{-1})	104.4 ± 5.89	96.67 ± 11.09
	(64.12–140.16)	(41.56–160.69)

Values are given as mean ± standard error (top) and range (bottom).

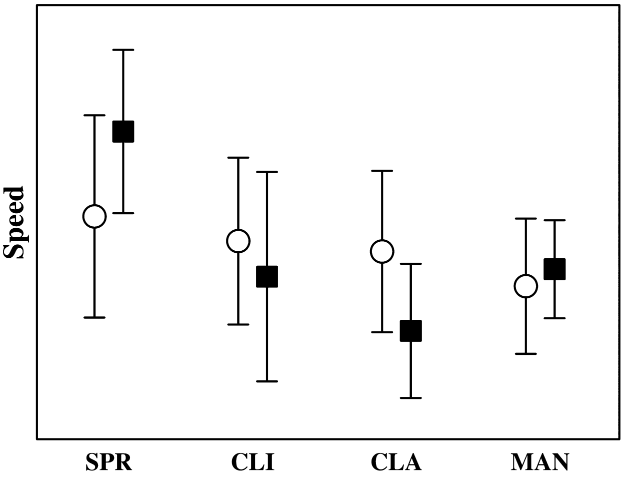

Figure 2 Least-squares means of instantaneous speed observed for each sex across the tested locomotion conditions (SPR, sprinting; CLI, climbing; CLA, clambering; MAN, manoeuvrability). Open circles, females; closed squares, males. Vertical bars denote 95% confidence intervals. Notice that here values are presented for instantaneous speeds, but statistical results were invariant when conducted on 10-cm interval speeds (see Table 1 and Results section).

Table 3 Results obtained from analyses of covariance on locomotor performance as multivariately represented by all measured speeds, with SEX as categorical predictor and SIZE or SHAPE as covariates

		Instantaneous speeds			10-cm interval speeds		
	d.f.	Pillai	*F*	*P*	Pillai	*F*	*P*
SEX	1	0.549	5.183	**0.006**	0.413	2.988	**0.048**
SIZE	1	0.287	1.711	0.194	0.263	1.515	0.242
SEX × SIZE	1	0.069	0.314	0.865	0.079	0.364	0.831
Residuals	20						
	d.f.	Pillai	F	*P*	Pillai	F	*P*
SEX	1	0.622	3.706	**0.048**	0.482	3.018	0.058
SHAPE	5	1.299	1.155	0.332	0.840	1.459	0.176
SEX × SHAPE	5	1.069	0.875	0.616	0.645	1.027	0.442
Residuals	12						

Significant effects are in bold. d.f., degrees of freedom for each effect; Pillai, Pillai's trace; *F*, approximate *F*-statistic; *P*, corresponding *P*-value.

traits. Nevertheless, our results also confirm that the relationship between morphology and performance is not always easy to assess based on biomechanical predictions, in accordance with previous interspecific observations on lacertids (Van Damme *et al*., 2003). While this study cannot disentangle the evolutionary mechanisms responsible for the SD observed, it adds an important piece to our understanding of the functional significance of morphological SD and provides some clues to the evolution of locomotor SD in these lizards.

Our results indicate significant SD in both body size and shape in *P. bocagei*. Indeed, males are larger in size, with relatively longer limbs, but relatively shorter trunks than females (Table 1, Fig. 1). These differences represent a widespread pattern of morphological SD in lizards (Braña, 1996; Olsson *et al*., 2002) and in *Podarcis* in specific (Braña, 1996; Kaliontzopoulou *et al*., 2010*a*,*b*). More importantly, our results also demonstrate that significant SD exists in locomotor performance in *P. bocagei* (Table 1), a pattern that has not been previously reported within this genus. Both when examining instantaneous and 10-cm interval speeds, we found that males exhibit significantly higher velocities when sprinting, as compared with climbing, clambering and manoeuvring through the pinboard (Fig. 2). In turn, females do not show a significant variation of their velocity across conditions. The increased sprinting speed observed in males as compared with other locomotion conditions may be associated with male behaviour during territorial defence: males patrolling territories, searching for mates, courting or engaging in mate-guarding are more exposed to predators (Castilla & Labra, 1998; Cooper Jr, 1999; Martín & López, 2001; Cooper Jr & Vitt, 2002), in which case natural selection would favour higher sprint speed and the morphological traits that enhance it. On the contrary, female lizards do not engage in such territorial activities and have been suggested to use crypsis more frequently to avoid predation (Schwarzkopf & Shine, 1992).

Furthermore, MANCOVA comparisons (Table 3) indicate that SD in locomotor performance in *P. bocagei* is not

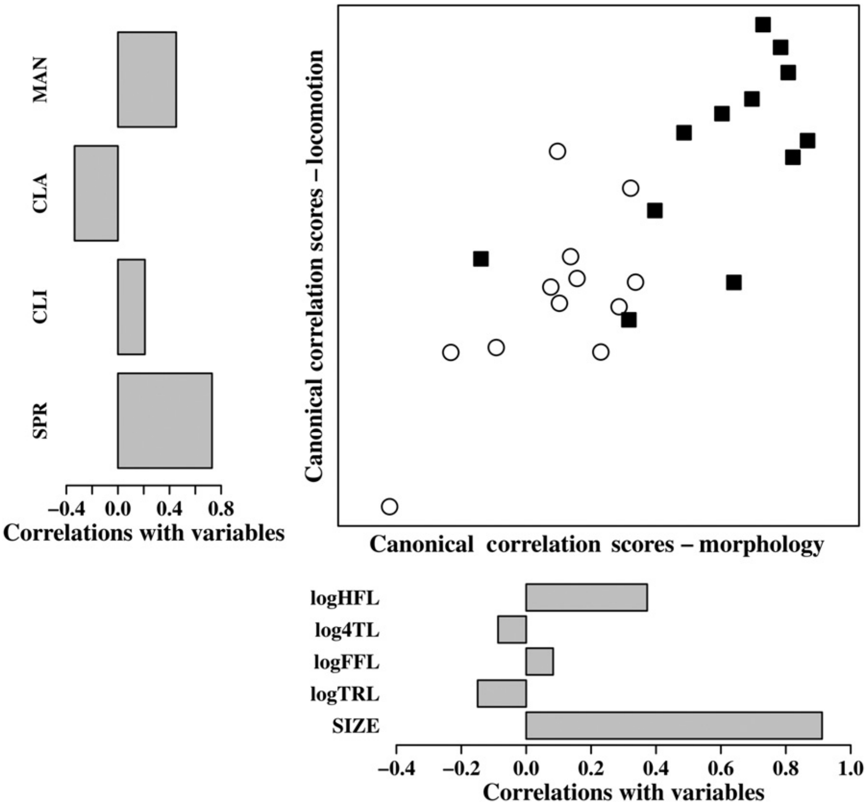

Figure 3 Scatter-plot of individual scores of females (open circles) and males (closed squares) obtained from canonical correlation analysis of morphological variables and instantaneous locomotor speeds. Bar-plots next to each axis represent the correlations observed between that axis and the variables included in each block. SIZE, total body size obtained by isometric projection; prjTRL, size-corrected trunk length; prjFLL, size-corrected fore limb length; prj4TL, size-corrected hind foot length; prjHLL, size-corrected hind limb length; SPR, sprinting; CLI, climbing; CLA, clambering; MAN, manoeuvrability.

explained by variation in body size between the sexes alone, as has been the case in other studies (Braña, 2003; Lailvaux, 2007), but rather involves both SIZE and SHAPE components of morphological SD, at least when considering instantaneous speeds. The same is suggested by canonical correlation analysis, where a strong association ($r \approx 0.80$) exists between morphology and instantaneous locomotor speeds, encompassing a positive contribution of body size and limb length on the morphological dimension and a positive contribution of sprint speed, climbing speed and manoeuvrability, but a negative contribution of clambering speed on the locomotor dimension (Fig. 3). Interestingly, while this type of analysis is not *a priori* informed on the sexual identity of individuals, a nearly complete segregation of both sexes is observed in the space of morphology-performance association (Fig. 3). These results are in general accordance with previous observations regarding lacertids (Van Damme *et al*., 2003). While other factors, including behaviour, thermal ecology, hormones or muscular physiology (Garland & Losos, 1994; Bauwens *et al*., 1995; Aerts *et al*., 2000; Lailvaux, 2007), may play an important role in determining locomotor SD, our results indicate that this is also strongly associated with morphological SD, supporting the idea that SD in both sets of traits may have coevolved. It is also important to notice that a difference exists between the results obtained considering instantaneous or 10-cm interval speeds in analyses examining morphology-performance associations. This is very likely due to a higher resolution and precision obtained through instantaneous speed calculation, as indicated by lower within-sex variances (Table 2). Indeed, speeds calculated across distance intervals are known to be highly influenced by locomotor mode and individual motivation (Braña, 2003), while instantaneous speeds would provide a more accurate descriptor of individual locomotor capacity.

From a functional perspective, the observed locomotor SD and its relation to morphological SD fits biomechanical predictions. Indeed, both larger body size and relatively longer limbs are known to enhance level running in several lizard species, by increasing stride length (Garland & Losos, 1994; Van Damme *et al*., 2003). In turn, both larger body size and longer limbs are thought to be detrimental during locomotion on an incline (Van Damme *et al*., 2003). First, increased body size in terms of SVL generally correlates to increased weight, which also augments the effect of gravity during climbing. Second, longer limbs may reduce speed in inclined planes, by elevating the centre of gravity away from the substrate and inducing higher instability (Vanhooydonck & Van Damme, 2001; Van Damme *et al*., 2003). Finally, a relatively longer trunk may increase manoeuvrability by enhancing body flexibility and allowing a more serpentine mode of locomotion (Arnold, 1998; Van Damme & Vanhooydonck, 2002; Van Damme *et al*., 2003). Thus, the larger body size, longer limbs and shorter trunk of male *P. bocagei* may explain the reduced speed attained by this sex on inclines and when manoeuvring through the pinboard. Indeed, such trade-offs have been previously explored across lizard species (Losos, Walton &

Bennett, 1993; Van Damme & Vanhooydonck, 2002; Van Damme *et al*., 2003), but to our knowledge, this is the first evidence that such a pattern may also exist within species.

From an evolutionary perspective, several, non-mutually exclusive hypotheses can explain the strong association between morphological and locomotor SD. First, given the importance of locomotor performance for habitat use and the marked morphological patterns that emerge from this association (Garland & Losos, 1994; Van Damme *et al*., 2003), one could predict differential habitat use between both sexes in *P. bocagei*, thus constituting an ecologically meaningful case of SD (Lailvaux & Vincent, 2007). While no such evidence exists for this species (AK & MAC, pers. obs.), an ecological causation or meaning for the observed SD cannot be dismissed without further investigation, particularly given that niche divergence is one of the main evolutionary hypotheses invoked to explain SD (Slatkin, 1984). Second, SD in both sets of traits may have evolved in a correlated manner under the effect of natural or sexual selection acting on male locomotion, to enhance territorial activities (Stamps, 1983; Husak & Fox, 2008). Finally, we cannot exclude the hypothesis that the SD observed in locomotion traits might be the side effect of other selective forces acting on morphology. For instance, part of the performance differences observed between the sexes could be attributed to the relatively longer trunk of females, a morphological difference that is known to emerge under the action of fecundity selection enhancing space for eggs (Olsson *et al*., 2002).

While our study supports the hypothesis that morphological and locomotor SD are tightly associated in *P. bocagei*, further investigation is in need to clarify the evolutionary basis of this relationship, but also to examine its generality. From an evolutionary perspective, examination of how male and female lizards employ their maximal locomotor capacities in nature under different ecological contexts may amplify or lessen the observed differences between the sexes and would shed light to the relative importance of sexual and natural selection as causal forces of both morphological and locomotor SD (Husak & Fox, 2008; Irschick *et al*., 2008). Similarly, the existence or lack of sexual divergence in microhabitat use would shed light into the potential role of niche segregation as an evolutionary agent of the observed patterns.

Acknowledgments

A.K. is supported by a post-doctoral grant (SFRH/BPD/68493/2010) from Fundação para a Ciência e Tecnologia (FCT, Portugal). D.C. Adams and two anonymous reviewers provided helpful comments on previous versions of the paper. The study was supported by the projects PTDC/BIA-BDE/67678/2006 and PTDC/BIA-BEC/101256/2008 funded by FCT. We thank Zoo Santo Inácio for providing the temperature-controlled room where performance experiments were carried out. Scientific capture and handling permits were provided by Instituto para a Conservação da Natureza e Biodiversidade (ICNB, Portugal). All experiments followed the ethical guidelines of the University of Porto.

References

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

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

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

Andersson, M. (1994). Sexual size dimorphism. In *Sexual selection: monographs in behaviour and ecology*: 247–293. Krebs, J.R. & Clutton-Brock, T.H. (Eds). Princeton, NJ: Princeton University Press.

Arnold, E.N. (1998). Structural niche, limb morphology and locomotion in lacertid lizards (Squamata, Lacertidae); a preliminary survey. *Bull. Br. Mus. Nat. Hist. (Zool.)* **64**, 63–89.

Bauwens, D., Garland, T.J., Castilla, A.M. & Van Damme, R. (1995). Evolution of sprint speed in lacertid lizards: morphological, physiological, and behavioral covariation. *Evolution* **49**, 848–863.

Braña, F. (1996). Sexual dimorphism in lacertid lizards: male head increase vs female abdomen increase? *Oikos* **75**, 511–523.

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**, 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**, 251–264.

Carretero, M.A., Ribeiro, R., Barbosa, D., Sá-Sousa, P. & Harris, D.J. (2006). Spermatogenesis in two Iberian *Podarcis* lizards: relationships with male traits. *Anim. Biol.* **56**, 1–12.

Castilla, A.M. & Labra, A. (1998). Predation and spatial distribution of the lizard *Podarcis hispanica atrata*: an experimental approach. *Acta Oecol.* **19**, 107–114.

Cooper, W.E. Jr (1999). Tradeoffs between courtship, fighting, and antipredatory behavior by a lizard, *Eumeces laticeps*. *Behav. Ecol. Sociobiol.* **47**, 54–59.

Cooper, W.E. Jr & Vitt, L.J. (2002). Increased predation risk while mate guarding as a cost of reproduction for male broad-headed skinks (*Eumeces laticeps*). *Acta Ethol.* **5**, 19–23.

Cullum, A.J. (1998). Sexual dimorphism in physiological performance of whiptail lizards (genus *Cnemidophorus*). *Physiol. Zool.* **71**, 541–552.

Fairbairn, D.J. (1997). Allometry for sexual size dimorphism: patterns and process in the coevolution of body size in males and females. *Annu. Rev. Ecol. Syst.* **28**, 659–687.

Galán, P. (2011). Comportamiento arborícola en *Podarcis bocagei*. *Bull. Asoc. Herpetol. Esp.* **22**, 54–56.

Garland, T.J. & Losos, J.B. (1994). Ecological morphology of locomotor performance in squamate reptiles. In *Ecological morphology: integrative organismal biology*: 240–302. Wainwright, P.C. & Reilly, S.M. (Eds). Chicago: University of Chicago Press.

Hothorn, T., Bretz, F. & Westfall, P. (2008). Simultaneous inference in general parametric models. *Biom. J.* **50**, 346–363.

Husak, J.F. (2006). Does speed help you survive? A test with collared lizards of different ages. *Funct. Ecol.* **20**, 174–179.

Husak, J.F. & Fox, S.F. (2008). Sexual selection on locomotor performance. *Evol. Ecol. Res.* **10**, 213–228.

Husak, J.F., Fox, S.F., Lovern, M.B. & Van Den Bussche, R.A. (2006). Faster lizards sire more offspring: sexual selection on whole-animal performance. *Evolution* **60**, 2122–2130.

Husak, J.F., Fox, S.F. & Van Den Bussche, R.A. (2008). Faster male lizards are better defenders not sneakers. *Anim. Behav.* **75**, 1725–1730.

Huyghe, K., Vanhooydonck, B., Scheers, H., Molina-Borja, M. & Van Damme, R. (2005). Morphology, performance and fighting capacity in male lizards, *Gallotia galloti*. *Funct. Ecol.* **19**, 800–807.

Innovision Systems Inc. (2007). *Maxmate: motion analysis toolbox for excel, v. 3.6*. Columbiaville, Michigan: Innovision Systems Inc..

Innovision Systems Inc. (2009). *Maxtraq 2D: video based tracking software, v. 2.13*. Columbiaville, Michigan: Innovision Systems Inc..

Iraeta, P., Monasterio, C., Salvador, A. & Díaz, J.A. (2011). Sexual dimorphism and interpopulation differences in lizard hind limb length: locomotor performance or chemical signalling? *Biol. J. Linn. Soc.* **104**, 318–329.

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

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**, 177–196.

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

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

Lailvaux, S.P. (2007). Interactive effects of sex and temperature on locomotion in reptiles. *Integr. Comp. Biol.* **47**, 189–199.

Lailvaux, S.P. & Irschick, D.J. (2006). A functional perspective on sexual selection: insights and future prospects. *Anim. Behav.* **72**, 263–273.

Lailvaux, S.P. & Irschick, D.J. (2007*a*). The evolution of performance-based male fighting ability in Caribbean *Anolis* lizards. *Am. Nat.* **170**, 573–586.

Lailvaux, S.P. & Irschick, D.J. (2007*b*). Effects of sex and temperature on jump performance and biomechanics in the lizard *Anolis carolinensis*. *Funct. Ecol.* **21**, 534–543.

Lailvaux, S.P. & Vincent, S.E. (2007). Ecological dimorphisms: an introduction to the symposium. *Integr. Comp. Biol.* **47**, 169–171.

Lailvaux, S.P., Alexander, G.J. & Whiting, M.J. (2003). Sex-based differences and similarities in locomotor performance, thermal preferences, and escape behaviour in the lizard *Platysaurus intermedius wilhelmi*. *Physiol. Biochem. Zool.* **76**, 511–521.

Lawrence, M.A. (2012). ez: easy analysis and visualization of factorial experiments. R package version 3.0-1. http://CRAN.R-project.org/package=ez

Legendre, P. & Legendre, L. (1998). *Numerical ecology*. 2nd English edn. Amsterdam: Elsevier.

Lindenfors, P., Gittleman, J.L. & Jones, K.E. (2007). Sexual size dimorphism in mammals. In *Sex, size and gender roles: evolutionary studies of sexual size dimorphism*: 16–26. Fairbairn, D.J., Blackenhorn, W.U. & Székely, T. (Eds). Oxford: Oxford University Press.

Losos, J.B., Walton, B.M. & Bennett, A.F. (1993). Trade-offs between sprinting and clinging ability in Kenyan chameleons. *Funct. Ecol.* **7**, 281–286.

Losos, J.B., Creer, D.A. & Schulte, II, J.A. (2002). Cautionary comments on the measurement of maximum locomotor capabilities. *J. Zool.* **258**, 57–61.

Martín, J. & López, P. (2001). Risk of predation may explain the absence of nuptial coloration in the wall lizard, *Podarcis muralis*. *Evol. Ecol. Res.* **3**, 889–898.

Maxwell, S.E. & Delaney, H.D. (1990). *Designing experiments and analyzing data: a model comparison perspective*. Belmont: Wadsworth.

Miles, D.B., Snell, H.L. & Snell, H.M. (2001). Intrapopulation variation in endurance of Galapagos lava lizards (*Microlophus albemarlensis*): evidence for an interaction between natural and sexual selection. *Evol. Ecol. Res.* **3**, 795–804.

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. http://CRAN.R-project.org/package=vegan

Olsson, M., Shine, R., Wapstra, E., Ujvari, B. & Madsen, T. (2002). Sexual dimorphism in lizard body shape: the roles of sexual selection and fecundity selection. *Evolution* **56**, 1538–1542.

R Development Core Team (2012). *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.

Rohlf, F.J. & Corti, M. (2000). Use of two-block partial least-squares to study covariation in shape. *Syst. Biol.* **49**, 740–753.

Schwarzkopf, L. & Shine, R. (1992). Costs of reproduction in lizards: escape tactics and susceptibility to predation. *Behav. Ecol. Sociobiol.* **31**, 17–25.

Slatkin, M. (1984). Ecological causes of sexual dimorphism. *Evolution* **38**, 622–630.

Snell, H.L., Jennings, R.D., Snell, H.M. & Harcourt, S. (1988). Intrapopulation variation in predator-avoidance performance of Galapagos lava lizards: the interaction of sexual and natural selection. *Evol. Ecol. Res.* **2**, 353–369.

Stamps, J. (1983). Sexual selection, sexual dimorphism and territoriality. In *Lizard ecology: studies of a model organism*: 169–204. Huey, R.B., Pianka, E.R. & Schoener, T.W. (Eds). Cambridge, MA: Harvard University Press.

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

Van Berkum, F.H. & Tsuji, J.S. (1987). Inter-familiar differences in sprint speed of hatching *Sceloporus occidentalis* (Reptilia: Lacertidae). *J. Zool. (Lond.)* **212**, 511–519.

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

Van Damme, R., Bauwens, D. & Verheyen, R.F. (1989). Effect of relative clutch mass on sprint speed in the lizard *Lacerta vivipara*. *J. Herpetol.* **23**, 459–461.

Van Damme, R., Bauwens, D. & Verheyen, R.F. (1990). Evolutionary rigidity of thermal physiology: the case of the temperate lizard *Lacerta vivipara*. *Oikos* **57**, 61–67.

Van Damme, R., Vanhooydonck, B., Aerts, P. & De Vree, F. (2003). Evolution of lizard locomotion: context and constraint. In *Vertebrate biomechanics and evolution*: 267–282. Bels, V., Gasc, J.P. & Casinos, A. (Eds). Oxford: BIOS Scientific Publishers.

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

Vanhooydonck, B. & Van Damme, R. (2003). Relationships between locomotor performance, microhabitat use and antipredator behaviour in lacertid lizards. *Funct. Ecol.* **17**, 160–169.