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Sexual dimorphism in traits related to locomotion: ontogenetic patterns of variation in *Podarcis* wall lizards

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Sexual dimorphism in body size and shape in animals is normally linked to sexual selection mechanisms that modify the morphological properties of each sex. However, sexual dimorphism of ecologically relevant traits may be amplified by natural selection and result in the ecological segregation of both sexes. In the present study, we investigated patterns of sexual dimorphism of morphological traits relevant for locomotion in two lacertid lizards, *Podarcis bocagei* and *Podarcis carbonelli*, aiming to identify ontogenetic sources of variation. We analysed trunk and limb variation in relation to total body size, as well as the covariation of different traits, aiming to shed light on the proximate causation of adult sexual dimorphism. We find that, although immatures are generally monomorphic, adult females have a longer trunk, and adult males have longer fore and hind limbs. Both sexes differ substantially with respect to their growth trajectories and relationships between traits, whereas, in some cases, there are signs of morphological constraints delimiting the observed patterns. Because of the direct connection between limb size/shape and locomotor performance, which is relevant both for habitat use and escape from predators, the observed patterns of sexual dimorphism are expected to translate into ecological differences between both sexes. © 2010 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2010, **99**, 530–543.

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INTRODUCTION

Sexual dimorphism, comprising the differentiation of males and females within a single species in morphology, physiology, performance, behaviour, or any other trait, has long been a paradigm for evolutionary biologists (Darwin, 1874; Andersson, 1994). Resulting from selection forces that act differentially on individuals of each sex, sexual dimorphism patterns provide an opportunity to increase our understanding of how organisms adapt to fulfil their reproductive, ecological, and social roles and enhance their fitness (Fairbairn, 1997). The most commonly evoked hypotheses to explain size sexual dimorphism are: (1) sexual selection usually favouring bigger body size in males when territoriality and male antagonistic behaviour are involved in female mate choice (Stamps, 1983; Cox, Skelly & John-Alder, 2005) and (2) natural selection favouring bigger body size in females when a positive correlation exists between female body size and progeny quantity and/or quality (Braña, 1996; Fairbairn, 1997; Olsson *et al.*, 2002; Du, Ji & Shine, 2005). Focusing on the variation of individual characters, sexual dimorphism in traits relevant for locomotion might evolve when territory defence plays an important role for mate acquisition (Stamps, 1983; Andersson, 1994; Perry *et al.*, 2004; Peterson & Husack, 2006).

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Sexual dimorphism in ecologically relevant traits is often considered to be initially driven by sexual selection acting on total body size, but is maintained and/or amplified by natural selection (Schoener, 1967; Slatkin, 1984; Shine, 1989; Andersson, 1994; Vincent & Herrel, 2007). A well known example of ecologically relevant sexual dimorphism in lizards is that of head size and shape; although such a pattern has evolved under the influence of sexual selection (Braña, 1996; Herrel, Van Damme & De Vree, 1996; Kaliontzopoulou, Carretero & Llorente, 2007, 2008a), it also frequently translates into sexual differences with respect to prey size and hardness (Herrel, De Grauw & Lemos-Espinal, 2001a; Herrel *et al.*, 2001b; Vincent & Herrel, 2007). In relation to traits relevant for locomotion, limb absolute and relative lengths, as well as the interlimb ratio, are known to be frequently dimorphic in lizards in general and lacertids in particular (Arnold, 1998; Kaliontzopoulou *et al.*, 2007; Brecko *et al.*, 2008). Sexual dimorphism in limb length has been principally related to an increased reproductive success through territory defence and maintenance (Stamps, 1983; Miles, Snell & Snell, 2001; Perry *et al.*, 2004; Peterson & Husack, 2006), but also to general fitness as determined by space and resource use (Arnold, 1983; Abell, 1999). From an ecological point of view, limb shape is highly relevant for lizard locomotion (Irschick, 2002; Toro *et al.*, 2003; Elstrott & Irschick, 2004; Vanhooydonck, Herrel & Irschick, 2006) and is thus under strong selective influence related to microhabitat use (Losos, 1990a, b; Thompson & Withers, 1997; Arnold, 1998; Aerts *et al.*, 2000) and, most importantly, to escape from predators (Schulte *et al.*, 2004; Irschick *et al.*, 2005; Vanhooydonck, Herrel & Irschick, 2007; Thompson & Withers, 2005). Nevertheless, few detailed data exist on the patterns of intraspecific variation and sexual dimorphism of these traits (Toro *et al.*, 2003; Brecko *et al.*, 2008).

This is also the case of female-biased trunk length dimorphism; in many lizard species, and particularly lacertids, females present a longer trunk as a result of fecundity (natural) selection, increasing the space available for eggs (Braña, 1996; Olsson *et al.*, 2002). Such an adaptation is frequently linked to sexual variation in the number of presacral vertebrae (Arnold, 1973, 1989; Kaliontzopoulou, Carretero & Llorente, 2008b). At the interspecific level, this trait has been related to manoeuvrability and is expected to affect locomotor performance (Van Damme & Vanhooydonck, 2002), possibly causing differential space use by both sexes in terms of microhabitat use. Therefore, although the study of sexual dimorphism patterns has largely concentrated on total body size, the separate study of different body parts and their integration can shed light into the underlying evolutionary mechanisms (Butler & Losos, 2002).

When looking for hints into the evolutionary mechanisms causing the morphological differentiation of both sexes, we cannot neglect the fact that different body parts are inevitably bound to be integrated towards the organisms' correct functioning and survival (i.e. selection acts over organisms as a whole and not on individual traits) (Eble, 2003; Klingenberg, 2008). A classic paradigm is the relationship between shape and size. Because of physiological, mechanical and morphogenetic constraints, the scaling of different characters with total body size normally results in different allometric relationships among body traits (D'Thompson, 1917; Sprent, 1972; Brown, West & Enquist, 2000). In the context of size variation, the ontogenetic processes shaping adult sexual dimorphism and the integration of body parts throughout ontogeny constitute crucial pieces of evidence that may help explain the underlying evolutionary mechanisms (Shine, 1990; Shea, 1992; Stamps, 1993; Hews, 1996; Watkins, 1996; Fairbairn, 1997).

In the present study, we investigate patterns of sexual dimorphism, ontogenetic trajectories and character scaling in traits relevant for locomotion in two lacertid lizards, *Podarcis bocagei* and *Podarcis carbonelli*, aiming to: (1) describe patterns of absolute and relative size sexual dimorphism; (2) explore the ontogenetic causes underlying patterns of variation; and (3) analyse the relationships between traits during development. An important sexual variation in relative trait size and mainly in ontogenetic trajectories and relationships between traits would indicate the influence of sexual selection mechanisms with respect to modifying traits relevant for locomotion under different rules in both sexes. By contrast, an absence of such differentiation would indicate that sexual variation in these traits is merely the result of body size variation and therefore is not a direct target of selective processes.

MATERIAL AND METHODS

STUDY ORGANISMS

Podarcis bocagei (Seoane 1884) and *P. carbonelli*, Pérez-Mellado 1981 are two lacertid species endemic to the western Iberian Peninsula. Initially considered as conspecific, the two species are now known to be both phylogenetically (Harris & Sá-Sousa, 2001, 2002; Pinho, Ferrand & Harris, 2006; Pinho, Harris & Ferrand, 2007) and morphologically (Sá-Sousa *et al.*, 2000; Sá-Sousa, 2001a; Sá-Sousa & Harris, 2002; Kaliontzopoulou *et al.*, 2005, 2008b) distinct, although relatively similar in terms of habitat use. They are members of the *P. hispanica* species complex (*sensu* Harris & Sá-Sousa, 2002), although they are both differentiated by the rest of the forms in being ground-dwelling, rather than saxicolous (Sá-Sousa, 2001a, b; Carretero *et al.*, 2002). Both species are known to present a marked size (Kaliontzopoulou *et al.*, 2007) and shape (Kaliontzopoulou *et al.*, 2008a) sexual dimorphism.

SPECIMENS EXAMINED

We studied a total of 97 *P. bocagei* females (67 adults and 30 immatures), 143 *P. bocagei* males (93 adults and 50 immatures), 126 *P. carbonelli* females (90 adults and 36 immatures), and 129 *P. carbonelli* males (104 adults and 25 immatures). Specimens of *P. bocagei* were collected in Mindelo-Vila Chã (UTM 29T NF27) and Espinho-Granja (UTM 29T NF24, NF34), whereas those of *P. carbonelli* were also collected in the later locality, as well as in Torreira (UTM 29T NF21). All three sites are characterized by similar climatic conditions (Direcção Geral do Ambiente, 1995) and habitat structure typical of Atlantic dunes (Barreto-Caldas, Honrado & Paiva, 1999). All animals were sacrificed by cold torpor, measured, and preserved in 96% alcohol. The sex and state of sexual maturity (treated as 'class') of the lizards were diagnosed by inspection of the reproductive organs after dissection in specimens caught during the reproductive season (Carretero *et al.*, 2006). For those captured outside the reproductive season, specimens were considered adults when exceeding the minimal adult snout–vent length (SVL) observed in each sex during the reproductive season (Carretero & Llorente, 1993). This resulted in four 'sex by class' groups for examination within each species: immature males, immature females, adult males, and adult females.

CHARACTER QUANTIFICATION

To describe the morphological properties of the studied individuals, we measured ten biometric characters to the nearest 0.01 mm using electronic callipers: SVL, trunk length (TRL), head length (HL), head width (HW), head height (HH), fore limb length (FFL), hind limb length (HFL), femur length (FL), tibia length (TBL), and length of the hind foot and fourth toe including the nail (4TL). More details on character definitions and the exact way of measurement used are provided elsewhere (Kaliontzopoulou *et al.*, 2007). We used the geometric-mean method of Mosimann (1970) on head dimensions and calculated head size (HS) as the third root of the product of HL, HW, and HH, aiming to include it in the total body size analyses as a biologically significant part of the body.

STATISTICAL ANALYSES

All variables were log-transformed prior to analyses to ensure normality and homoscedasticity for all the groups and variables examined (Lilliefors test, $P > 0.1$; Levene's test, $P > 0.05$ in all cases). Data from both species examined were always treated separately. We used analysis of variance (ANOVA) comparisons considering the effect of sex, class, and their interaction to quantify sexual and ontogenetic morphological differentiation in locomotion-related traits (i.e. TRL, FFL, FL, TBL, 4TL, and HFL; see above). To remove the effect of size, and because we were interested in variation of different body parts, we used the method of Burnaby (1966) for multivariate size correction. For this purpose, we performed a principal components analysis on the eight quantified body measurements, considering all specimens of each species separately, and considered the first principal component as multivariate size (Rohlf & Bookstein, 1988). Note that, although head dimorphism in these species has been treated in detail elsewhere (Kaliontzopoulou *et al.*, 2007, 2008a) and is not examined in the present study, we included an estimate of HS in our calculation of multivariate body size because such an approach is more realistic biologically. We then projected initial variables relevant for locomotion orthogonally onto this vector to obtain 'size-free' variables. We performed an ANOVA considering the effect of sex, class, and their interaction on these projected variables to examine sexual and ontogenetic differentiation of body parts independently of size variation.

We used regression analyses to describe the ontogenetic trajectories of the relative size of body parts related to locomotion on multivariate body size, as well as to examine relationships between different traits independently of size variation. Integration of different body parts was investigated using two sets of analyses: regression of FFL and HFL on TRL, considering size-free traits, was used to examine the covariation patterns between structural parts of the body. Second, regression of FFL, FL, TBL, and 4TL on HFL, also considering size-free traits, was used to describe the relationships between fore and hind limbs, as well as between different hind limb segments. In all cases, species were treated separately and regression slopes were calculated for each sex separately, including both immature and adult specimens.

Because both dependent and independent variables were subject to measurement error, ordinary least squares regression will provide biased values of the regression estimates (McArdle, 1988; Sokal & Rohlf, 1995). Therefore, we applied reduced major axis regression (RMA). We used the (S)MATR software, version 1 (Falster, Warton & Wright, 2006) to calculate RMA regression estimates and test for deviations from isometry (slope equal to 1) and homogeneity of slopes between sexes. Because 'size-free' traits were examined, the lack of a relationship between any given pair of traits would indicate a proportional increase of these traits during growth, suggesting their integration through body size. Conversely, an isometric relationship between different 'size-free' traits would indicate that, although body parts grow more than expected as a result of size variation alone, a similar scaling with total body size is observed for both traits examined. Finally, a deviation from isometry for 'size-free' traits would indicate that body parts grow more than expected only as a result of size variation, and following divergent scaling relationships.

When common slopes allowed further comparisons between sexes, we performed tests of equality of intercepts and shifts along the common slopes between sexes, *sensu* Warton *et al.* (2006). Because the same datasets were used for multiple analyses (Curran-Everett, 2000), we used the false discovery rate procedure to adjust the observed *P*-values (Benjamini & Hochberg, 1995).

RESULTS

The first principal component of biometric variation within each species presented very high loadings of the same sign and magnitude with all the biometric variables taken into account, thus giving a good multivariate representation of multivariate body size (Table 1). The effect of both sex and class, as well as their interaction, were statistically significant for all the variables examined in both species, with the exception of the interaction term for TRL in both species (Table 2). Post-hoc comparisons indicated that multivariate size (PC1) varied between both sexes and classes, with adults obviously being larger than immatures for both sexes and adult males being larger than adult females [Unequal *N* honestly significant difference (HSD); $P < 0.001$ in all comparisons]. However, immatures are not dimorphic for multivariate size HSD; $P = 0.081$ for *P. bocagei* and $P = 0.91$ for *P. carbonelli*]. Considering individual traits, adults are sexually dimorphic for all the characters studied (unequal *N* HSD; $P < 0.01$, with the exception of TRL in *P. bocagei*, $P = 0.93$), whereas immatures are not dimorphic for any of them (unequal *N* HSD; $P > 0.05$ in all cases). Adults and immatures of the same sex always presented significant differences (unequal *N* HSD; $P < 0.001$ in all cases). Patterns are more complex for size-free characters. Although the effect of sex was always significant, this was not true for the effect of class and their interaction (Table 3). Considering body proportions, females had a relatively higher TRL for both immatures and adults and adult females had relatively higher TRL values than immatures (unequal *N* HSD; $P < 0.001$ in all cases), although differences were not significant between immature and adult males of neither species (unequal *N* HSD; $P = 0.99$ for *P. bocagei* and $P = 0.95$ for *P. carbonelli*). For relative FFL, adult females showed significantly lower values than adult males in *P. bocagei* (unequal *N* HSD; $P = 0.001$) and also compared to all other groups in *P. carbonelli* (unequal *N* HSD; $P < 0.001$ in all cases). For relative HFL and hind limb parts, adult females also showed lower values than other sex-class groups in both species (unequal *N* HSD; $P < 0.001$ in all cases), with the exception of TBL, which was not different in any of the groups examined in either species (unequal *N* HSD; $P > 0.1$ in all cases).

Table 1. Correlations of the biometric variables with the first principal component (multivariate body size) in each species

	*Podarcis bocagei**	*Podarcis carbonelli*†
logSVL	0.983	0.965
logTRL	0.929	0.856
logHS	0.986	0.981
logFFL	0.989	0.978
logFL	0.978	0.960
logTBL	0.971	0.963
log4TL	0.972	0.956
logHFL	0.990	0.983

*Eigenvalue = 0.093; 94.82% of variance explained.
†Eigenvalue = 0.055; 91.01% of variance explained.
SVL, snout–vent length; TRL, trunk length; HS, head size; FFL, fore limb length; FL, femur length; TBL, tibia length; 4TL, length of the hind foot and fourth toe including the nail; HFL, hind limb length.

ONTOGENY OF BODY PARTS

Regression of different body parts on multivariate body size (PC1) gave visibly distinct patterns between both sexes in both species examined (Fig. 1, Table 4). Relative TRL increased with increasing PC1 in females of both species, under slopes that were significantly higher than those of males (Fig. 1A, B, Table 4). Males of *P. bocagei* did not present a significant relationship between relative TRL and PC1, indicating that TRL variation was as a result of body size variation alone. FFL only showed a significant negative relationship with PC1 in females of *P. carbonelli*, whereas regression estimates were not significant for the remaining groups (Fig. 1C, D, Table 4). Finally, variation of relative HFL was common in both species, with females showing a significant negative slope with PC1 and males lacking a significant relationship (Fig. 1E, F, Table 4).

Table 2. Descriptive statistics of biometric variables (log-transformed) for immature and adult females and males of both species studied

	Podarcis bocagei (d.f. = 239)					
	Immature females (*N* = 30)	Immature males (*N* = 50)	Adult females (*N* = 67)	Adult males (*N* = 93)	*F*	*P*
PC1 (size)	0.992 ± 0.010	1.020 ± 0.011	1.144 ± 0.003	1.213 ± 0.003	57.318	< 0.001
	0.884–1.070	0.872–1.146	1.074–1.198	1.119–1.279	734.049	< 0.001
					10.309	0.003
log (TRL)	1.236 ± 0.014	1.202 ± 0.013	1.423 ± 0.005	1.417 ± 0.005	5.18	0.026
	1.053–1.352	0.962–1.366	1.311–1.528	1.301–1.516	513.75	< 0.001
					2.46	0.118
log (FFL)	1.051 ± 0.011	1.072 ± 0.012	1.196 ± 0.003	1.267 ± 0.003	44.25	< 0.001
	0.928–1.137	0.889–1.223	1.115–1.240	1.186–1.335	599.99	< 0.001
					13.76	< 0.001
log (FL)	0.697 ± 0.014	0.720 ± 0.014	0.856 ± 0.006	0.952 ± 0.004	44.62	< 0.001
	0.481–0.808	0.497–0.891	0.728–0.956	0.823–1.046	478.72	< 0.001
					16.72	< 0.001
log (TBL)	0.515 ± 0.014	0.551 ± 0.016	0.701 ± 0.004	0.793 ± 0.005	47.78	< 0.001
	0.262–0.628	0.314–0.760	0.633–0.773	0.652–0.888	529.75	< 0.001
					9.31	0.004
log (4TL)	0.968 ± 0.012	0.988 ± 0.014	1.093 ± 0.004	1.173 ± 0.003	41.20	< 0.001
	0.803–1.061	0.699–1.138	1.024–1.151	1.088–1.261	398.44	< 0.001
					14.86	< 0.001
log (HFL)	1.250 ± 0.012	1.276 ± 0.013	1.393 ± 0.003	1.475 ± 0.003	52.44	< 0.001
	1.082–1.350	1.050–1.414	1.324–1.441	1.386–1.539	527.53	< 0.001
					14.38	< 0.001
	Podarcis carbonelli (d.f. = 254)					
	Immature females (*N* = 36)	Immature males (*N* = 25)	Adult females (*N* = 90)	Adult males (*N* = 104)	*F*	*P*
PC1 (size)	0.961 ± 0.011	0.969 ± 0.011	1.093 ± 0.003	1.145 ± 0.004	22.358	< 0.001
	0.810–1.058	0.846–1.049	1.015–1.168	1.033–1.231	580.891	< 0.001
					12.014	0.002
log (TRL)	1.227 ± 0.013	1.188 ± 0.014	1.391 ± 0.005	1.359 ± 0.005	18.30	< 0.001
	1.000–1.340	1.027–1.313	1.266–1.492	1.204–1.453	397.59	< 0.001
					0.15	0.725
log (FFL)	1.039 ± 0.010	1.048 ± 0.009	1.150 ± 0.003	1.213 ± 0.004	37.69	< 0.001
	0.899–1.134	0.917–1.116	1.083–1.217	1.098–1.280	547.52	< 0.001
					21.09	< 0.001
log (FL)	0.677 ± 0.013	0.700 ± 0.014	0.808 ± 0.005	0.891 ± 0.005	41.72	< 0.001
	0.480–0.816	0.543–0.816	0.702–0.903	0.757–0.989	390.96	< 0.001
					13.92	< 0.001
log (TBL)	0.501 ± 0.013	0.528 ± 0.013	0.661 ± 0.004	0.734 ± 0.006	35.14	< 0.001
	0.290–0.632	0.389–0.616	0.563–0.757	0.583–0.863	473.10	< 0.001
					7.64	0.007
log (4TL)	0.959 ± 0.010	0.977 ± 0.009	1.060 ± 0.003	1.127 ± 0.004	53.80	< 0.001
	0.823–1.069	0.897–1.056	0.989–1.124	1.025–1.202	472.95	< 0.001
					18.84	< 0.001
log (HFL)	1.240 ± 0.010	1.256 ± 0.011	1.355 ± 0.003	1.425 ± 0.004	50.60	< 0.001
	1.103–1.338	1.147–1.342	1.285–1.423	1.340–1.506	563.45	< 0.001
					20.76	< 0.001

Values shown are the mean ± SE (top), range (bottom). *F*- and *P*-values correspond to analysis of variance comparisons considering the effect of sex (top), class (middle) and their interaction (bottom). All *P*-values presented were corrected for multiple testing using the false discovery rate procedure.

TRL, trunk length; FFL, fore limb length; HS, head size; FL, femur length; TBL, tibia length; 4TL, length of the hind foot and fourth toe including the nail; HFL, hind limb length.

Table 3. Descriptive statistics of projected ('size-free') biometric variables for immature and adult females and males of both species studied

	Podarcis bocagei (d.f. = 239)					
	Immature females (*N* = 30)	Immature males (*N* = 50)	Adult females (*N* = 67)	Adult males (*N* = 93)	*F*	*P*
TRL	0.260 ± 0.005	0.213 ± 0.004	0.289 ± 0.003	0.214 ± 0.003	252.962	< 0.001
	0.212–0.298	0.145–0.250	0.221–0.353	0.129–0.296	15.606	< 0.001
					13.508	< 0.001
FFL	0.148 ± 0.002	0.154 ± 0.002	0.148 ± 0.002	0.157 ± 0.001	15.090	< 0.001
	0.116–0.180	0.126–0.183	0.120–0.189	0.123–0.190	0.320	0.601
					0.314	0.601
FL	–0.379 ± 0.005	–0.374 ± 0.003	–0.395 ± 0.003	–0.375 ± 0.002	15.201	< 0.001
	–0.442 to –0.342	–0.426 to –0.334	–0.461 to –0.344	–0.423 to –0.325	6.437	0.018
					5.132	0.034
TBL	–0.615 ± 0.004	–0.597 ± 0.005	–0.614 ± 0.004	–0.601 ± 0.003	14.284	< 0.001
	–0.660 to –0.559	–0.649 to –0.523	–0.678 to –0.552	–0.660 to –0.535	0.126	0.723
					0.404	0.601
4TL	0.089 ± 0.004	0.099 ± 0.003	0.072 ± 0.002	0.091 ± 0.002	24.548	< 0.001
	0.047–0.119	0.060–0.132	0.030–0.116	0.038–0.148	17.904	< 0.001
					1.982	0.215
HFL	0.319 ± 0.002	0.332 ± 0.001	0.311 ± 0.001	0.328 ± 0.001	67.553	< 0.001
	0.287–0.348	0.309–0.349	0.278–0.339	0.287–0.360	9.703	0.003
					1.139	0.363

	Podarcis carbonelli (d.f. = 254)					
	Immature females (*N* = 36)	Immature males (*N* = 25)	Adult females (*N* = 90)	Adult males (*N* = 104)	*F*	*P*
TRL	0.322 ± 0.005	0.276 ± 0.006	0.362 ± 0.003	0.280 ± 0.002	248.322	< 0.001
	0.238–0.373	0.197–0.326	0.282–0.432	0.219–0.344	28.954	< 0.001
					19.049	< 0.001
FFL	0.162 ± 0.002	0.164 ± 0.002	0.153 ± 0.002	0.168 ± 0.001	15.091	< 0.001
	0.127–0.184	0.146–0.186	0.114–0.188	0.129–0.204	1.372	0.265
					9.524	0.003
FL	–0.398 ± 0.004	–0.385 ± 0.005	–0.415 ± 0.003	–0.391 ± 0.002	26.131	< 0.001
	–0.460 to –0.342	–0.424 to –0.327	–0.489 to –0.358	–0.449 to –0.345	9.889	0.003
					2.309	0.149
TBL	–0.659 ± 0.004	–0.642 ± 0.005	–0.657 ± 0.003	–0.647 ± 0.003	10.894	0.002
	–0.698 to –0.598	–0.702 to –0.610	–0.713 to –0.572	–0.708 to –0.553	0.286	0.593
					0.703	0.421
4TL	0.138 ± 0.003	0.149 ± 0.003	0.126 ± 0.002	0.149 ± 0.002	34.755	< 0.001
	0.098–0.166	0.116–0.190	0.055–0.171	0.089–0.190	4.152	0.052
					4.832	0.037
HFL	0.326 ± 0.002	0.334 ± 0.002	0.315 ± 0.001	0.335 ± 0.001	58.323	< 0.001
	0.305–0.348	0.312–0.352	0.278–0.351	0.304–0.365	6.767	0.015
					11.483	0.002

Values shown are the mean ± SE (top), range (bottom). *F*- and *P*-values correspond to analysis of variance comparisons considering the effect of sex (top), class (middle) and their interaction (bottom). All *P*-values presented were corrected for multiple testing using the false discovery rate procedure.

TRL, trunk length; FFL, fore limb length; HS, head size; FL, femur length; TBL, tibia length; 4TL, length of the hind foot and fourth toe including the nail; HFL, hind limb length.

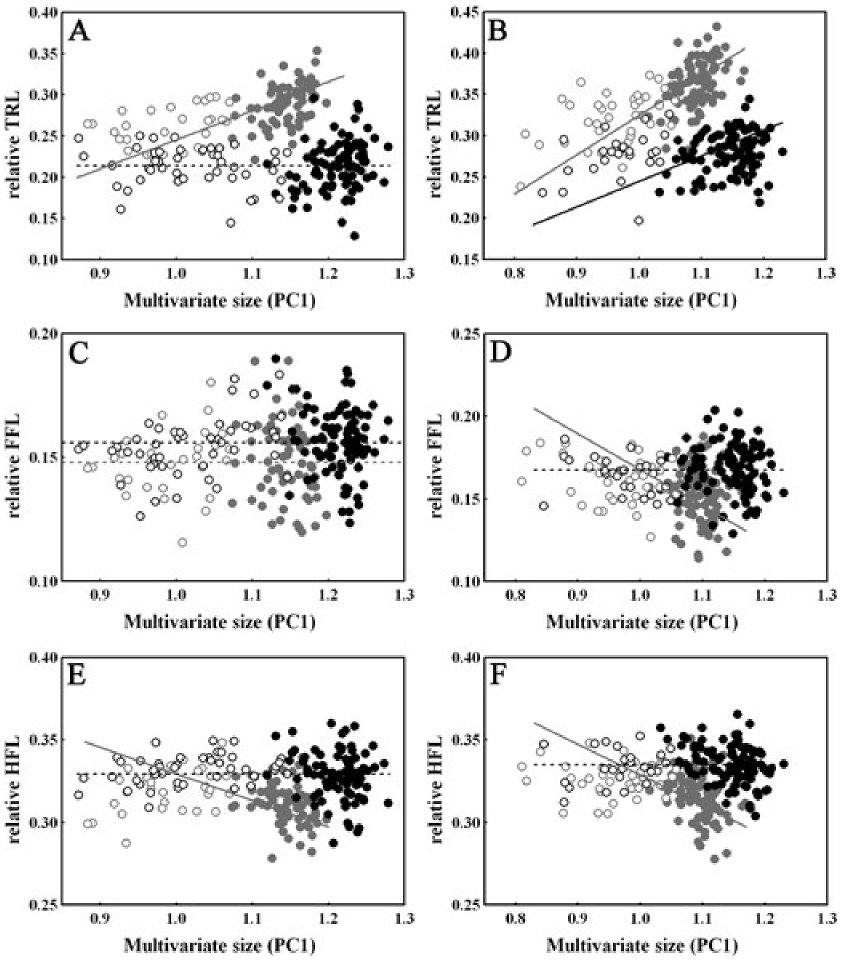

Figure 1. Ontogenetic relationship of relative trunk length (TRL; A, B), relative fore limb length (FFL; C, D) and hind limb length (HFL; E, F) with total body size (PC1) in *Podarcis bocagei* (left) and *Podarcis carbonelli* (right) for females (grey line) and males (black line). Grey circles, females; black circles, males; closed circles, adults; open circles, immatures. A dashed line represents a lack of significant relationships between both variables (Table 4).

Table 4. Regression results for the ontogenetic relationship of relative TRL, FFL, and HFL with total body size (PC1) in females (F) and males (M) of the two species studied

	Podarcis bocagei ($N_f = 97$, $N_m = 143$)						*Podarcis carbonelli* ($N_f = 126$, $N_m = 129$)				
	Sex	R^2	p	b	a		Sex	R^2	p	b	a
TRL	F	0.323	< 0.001	0.353	–0.107	TRL	F	0.408	< 0.001	0.477*	–0.152
	M	0.001	0.693	–	–		M	0.038	0.027	0.307*	–0.062
FFL	F	0.000	0.918	–	–	FFL	F	0.103	< 0.001	–0.218	0.385
	M	0.013	0.182	–	–		M	0.001	0.705	–	–
HFL	F	0.046	0.037	–0.161	0.490	HFL	F	0.166	< 0.001	–0.185	0.514
	M	0.014	0.169	–	–		M	0.003	0.525	–	–

*Test for common slopes: $F = 15.421$, $P < 0.001$.

N_f and N_m, sample size for females and males, respectively. R^2, squared correlation coefficient; p, P-value of R^2; b, slope; a, intercept. All P-values presented were corrected for multiple testing using the false discovery rate procedure.

TRL, trunk length; FFL, fore limb length; HFL, hind limb length.

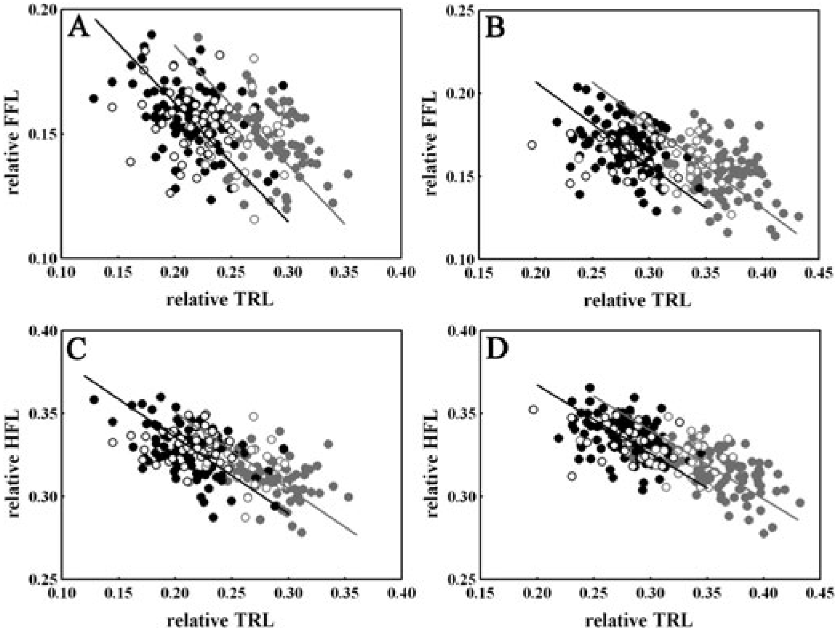

Figure 2. Relationship of relative fore (FFL; A, B) and hind limb length (HFL; C, D) with relative trunk length (TRL) in *Podarcis bocagei* (left) and *Podarcis carbonelli* (right) for females (grey line) and males (black line). Grey circles, females; black circles, males; closed circles, adults; open circles, immatures. A dashed line represents a lack of significant relationships between both variables (Table 5).

CHARACTER COVARIATION

Investigation of the relationships between different body parts through a regression of relative limbs' lengths (FFL and HFL) on relative TRL gave similar results in both species. Both relative FFL and relative HFL decreased under a common slope in both sexes with increasing relative TRL, although females of both species showed significantly higher intercepts than conspecific males (Fig. 2, Table 5).

Concerning interlimb relationships and variation of hind limb segments, patterns were also similar in both species examined. Relative FFL increased isometrically with increasing relative HFL in both sexes of both species (Fig. 3A, B, Table 5), although females of both species showed slightly higher intercept estimates than males. Relative FL and relative TBL did not show a significant relationship with relative HFL in any of the groups examined (Fig. 3C, D, E, F, Table 5). Finally, relative 4TL increased under a common, hypermetric slope in both sexes of both species examined (Fig. 3G, H, Table 5) and, again, females showed slightly higher intercept estimates compared to males.

DISCUSSION

The combined examination of sexual and ontogenetic variation can provide important insights into the causation and structural relationships of character covariation (Shine, 1990; Cox *et al.*, 2005). The results obtained in *P. bocagei* and *P. carbonelli* indicate important sexual and ontogenetic variation in terms of body shape and character covariation, giving hints into the possible interactions of sexual and natural selection. In terms of absolute character variation, the results are in accordance with previous observations for lacertid lizards (Braña, 1996; Arnold, 1998): adults are highly dimorphic, with males having longer fore and hind limbs, whereas females have longer trunks. By contrast, immatures of both species are monomorphic. Similar patterns are observed for size-free traits: adults are dimorphic, with both sexes having different body proportions for all the characters studied, although immatures are monomorphic in body shape except for relative trunk length.

ONTOGENY AND SEXUAL DIMORPHISM

The comparison of sexual dimorphism patterns in immatures and adults of *P. bocagei* and *P. carbonelli* neatly illustrates how different characters may come to be dimorphic under different mechanisms (Stamps, 1993). Although adult dimorphism in limb proportions is determined by sexually divergent growth patterns, trunk variation is rather 'intrinsic', being already evident in immatures. Here, fecundity selection enhancing space for the allocation of eggs in

Table 5. Regression results for the relationship of relative FFL and HFL with relative TRL and the relationship of relative FFL, FL, TBL and 4TL with relative HFL in females (F) and males (M) of the two species studied

	Podarcis bocagei ($N_\mathrm{f} = 97$, $N_\mathrm{m} = 143$)										
X = TRL	Sex	R^2	p	b	a	$F(b)$	$p(b)$	B	a-group	$F(a)$	p(a)
FFL	F	0.057	0.020	–0.490	0.285	0.118	0.731	–0.477	0.281	61.115	< 0.001
	M	0.093	< 0.001	–0.469	0.256				0.258		
HFL	F	0.166	< 0.001	–0.456	0.441	0.024	0.874	–0.461	0.443	31.226	< 0.001
	M	0.140	< 0.001	–0.465	0.429				0.428		
X = HFL	Sex	R^2	p	b	a	$F(b)$	$p(b)$	B	a-group	$F(a)$	p(a)
FFL	F	0.065	0.013	1.073	–0.189	0.222	0.638	1.035*	–0.177	10.075	0.002
	M	0.037	0.024	1.008	–0.176				–0.185		
FL	F	0.030	0.092	–	–	–	–	–	–	–	–
	M	0.011	0.228	–	–	–	–	–	–	–	–
TBL	F	0.000	0.880	–	–	–	–	–	–	–	–
	M	0.006	0.386	–	–	–	–	–	–	–	–
4TL	F	0.273	< 0.001	1.605	–0.426	0.080	0.778	1.637**	–0.436	10.303	0.001
	M	0.388	< 0.001	1.656	–0.452				–0.446		
	Podarcis carbonelli ($N_\mathrm{f} = 126$, $N_\mathrm{m} = 129$)										
X = TRL	Sex	R^2	p	b	a	$F(b)$	$p(b)$	B	a-group	$F(a)$	p(a)
FFL	F	0.196	< 0.001	–0.457	0.316	3.332	0.066	–0.505	0.333	66.219	< 0.001
	M	0.074	0.002	–0.566	0.325				0.308		
HFL	F	0.344	< 0.001	–0.388	0.4548	1.783	0.182	–0.414	0.464	34.572	< 0.001
	M	0.114	< 0.001	–0.451	0.465				0.45		
X = HFL	Sex	R^2	p	b	a	$F(b)$	$p(b)$	B	a-group	$F(a)$	p(a)
FFL	F	0.154	< 0.001	1.176	–0.219	0.306	0.582	1.214†	–0.231	9.933	0.002
	M	0.032	0.044	1.257	–0.254				–0.239		
FL	F	0.001	0.725	–	–	–	–	–	–	–	–
	M	0.002	0.625	–	–	–	–	–	–	–	–
TBL	F	0.003	0.527	–	–	–	–	–	–	–	–
	M	0.014	0.058	–	–	–	–	–	–	–	–
4TL	F	0.416	< 0.001	1.502	–0.349	0.364	0.547	1.545††	–0.362	5.657	0.017
	M	0.283	< 0.001	1.598	–0.386				–0.368		

*Test for deviation from isometry: $F = 0.278$, $P = 0.673$.

**Test for deviation from isometry: $F = 47.329$, $P < 0.001$.

†Test for deviation from isometry: $F = 3.889$, $P = 0.051$.

††Test for deviation from isometry: $F = 39.142$, $P < 0.001$.

X, X variable used in each set of regression analyses.

N_f and N_m, sample size for females and males, respectively. R^2, squared correlation coefficient; p, P-value of R^2; b, slope; a, intercept; $F(b)$ and $p(b)$, statistical F- and P-values of the test for common slopes between sexes; B, common slope; a-group, intercept of each sex under a common slope; $F(a)$ and $p(a)$, statistical F- and P-values of the test for common intercepts under a common slope B. All P-values presented were corrected for multiple testing using the false discovery rate procedure.

TRL, trunk length; FFL, fore limb length; HFL, hind limb length; FL, femur length; TBL, tibia length; 4TL, length of the hind foot and fourth toe including the nail.

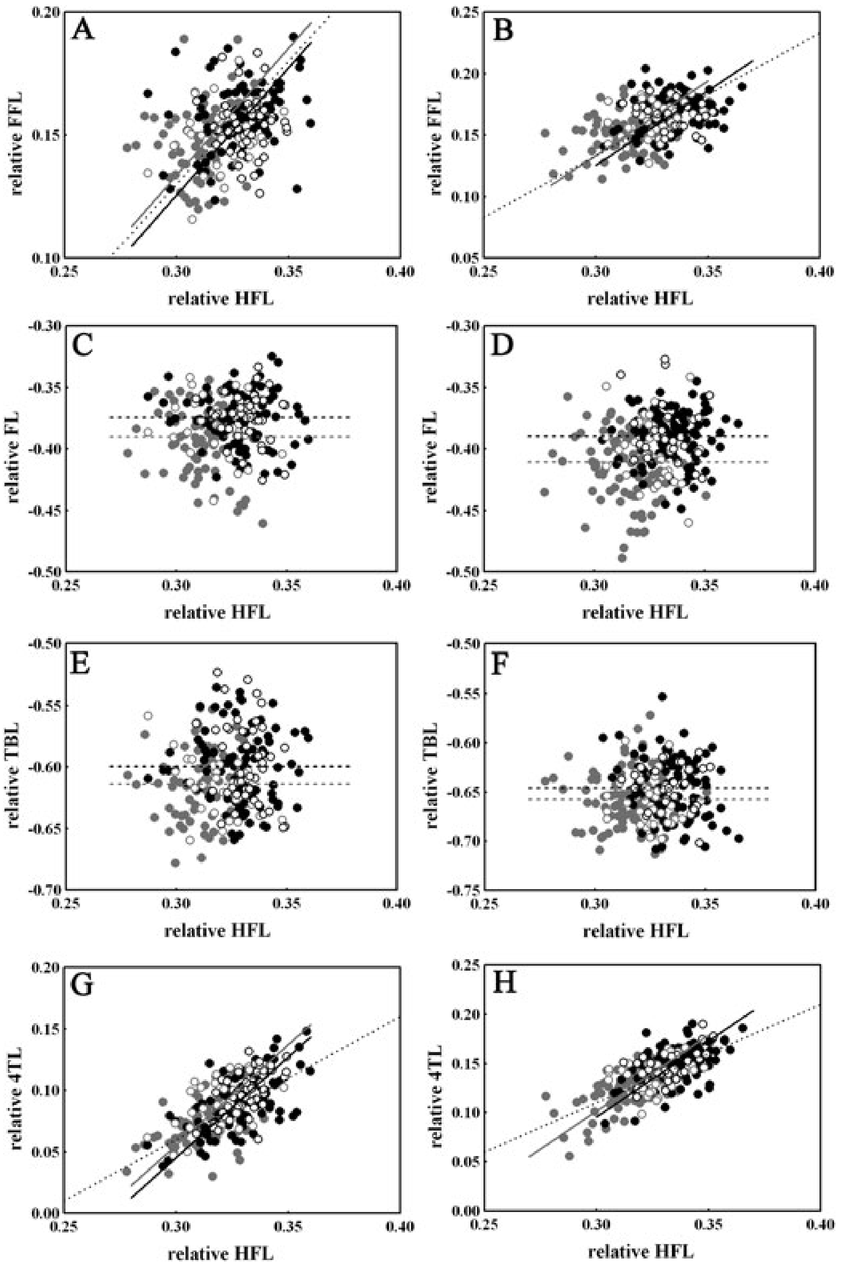

Figure 3. Relationship of relative fore limb length (FFL; A, B), relative femur length (FL; C, D), relative tibia length (TBL; E, F) and relative hind foot length (4TL; G, H) with relative hind limb length (HFL) in *Podarcis bocagei* (left) and *Podarcis carbonelli* (right) for females (grey line) and males (black line). Grey circles, females; black circles, males; closed circles, adults; open circles, immatures. A dashed line represents a lack of significant relationships between both variables (Table 5). A dotted line represents the expected relationship for isometry.

females is probably the driving force of sexual dimorphism (Braña, 1996; Olsson *et al.*, 2002). Such an adaptation is reached through the increase of the number of presacral vertebrae in females (Arnold, 1973, 1989; Kaliontzopoulou *et al.*, 2008b). Because the number of vertebrae is ontogenetically invariant, trunk length is bound to be relatively longer in females from early life stages. Interestingly, sexual dimorphism in this trait is further amplified during ontogeny: relative trunk length was found to be higher in adults than in immatures for females, but not for males. Additionally, females show a disproportionate increase of relative trunk length in relation to total body size (Fig. 1A, B). Such a pattern may be a result of differential growth allocation in both sexes (Stamps, 1993) and could be anatomically achieved by the increase of either vertebrae length or intervertebral spaces (Arnold, 1973; Van Damme & Vanhooydonck, 2002).

Concerning the ontogeny of limb traits, important differences also exist between both sexes. In this case, the starting point of the ontogenetic trajectories is common for both sexes, although different ending points are attained. However, the observed differences could be exclusively a result of total body size variation. The results obtained in the present study indicate that this is not the case; globally, females present negative ontogenetic slopes for relative limbs' proportions, whereas males lack a significant relationship between total body size and relative limbs' size (Fig. 1C, D, E, F, Table 4). Consequently, the sexual dimorphism patterns observed in adults are rather the result of distinct growth trajectories between sexes and not merely a result of total body size sexual dimorphism.

TRUNK LENGTH VARIATION: POTENTIAL CONSEQUENCES FOR LOCOMOTION

The important sexual and ontogenetic variation observed for both absolute and relative trunk length is expected to have implications for locomotion. At the interspecific level, a higher vertebrae number and longer trunk has been shown to enhance manoeuvrability and has been associated with habitat use (Arnold, 1998; Van Damme & Vanhooydonck, 2002). At the intraspecific level, however, the effect of possessing a longer trunk has never been analysed. In terms of locomotion, female *Podarcis* would be expected to perform a more 'serpentine' way of moving (Jayne, 1982, 1988a, b). That is, a longer trunk may suggest a greater relative input of body undulations (compared to limbs) with respect to locomotory propulsion. In this way, females would take advantage of their higher body flexibility in equivalence to that observed in species living in densely vegetated habitats (Arnold, 1998), and thus possibly increase stride length (Ritter, 1992; Russell & Bels, 2001), also compensating for their shorter limbs. A detailed analysis of sexual variation in locomotor behaviour and kinematics in *Podarcis* is necessary to confirm whether this marked morphological differentiation between sexes is reflected in their locomotion.

In addition, because it comprises the structurally 'central' part of the body, the trunk can be considered as the structure through which fore and hind limbs are linked and coordinated (Russell & Bels, 2001) Our analyses of relative limb length versus relative trunk length point to an integration of these characters. Independently of their sex, lizards of both species presented a negative allometric relationship between relative limb and trunk lengths, most likely indicating a structural restriction. The coupling of shorter limbs with longer trunk lengths may help to lower the centre of balance, aiming to compensate for the biomechanical restrictions posed by a longer trunk (Alexander, 1982; Farley & Ko, 1997), although such a hypothesis needs to be investigated further.

LIMB INTEGRATION AND SEGMENT VARIATION

The examination of the integration of fore and hind limbs in *Podarcis* lizards revealed that both sexes follow common patterns in this aspect. Although a marked sexual dimorphism exists in fore and hind limb length, the relative sizes of both extremities follow similar scaling rules in both sexes (Fig. 3A, B). As previously observed in lacertids (Arnold, 1998), females have higher interlimb ratios. Nevertheless, increase of fore and hind limb length appear to be uniform across sexes and proportional. Therefore, bigger body size does not seem to promote differential growth of fore versus hind limbs, suggesting that the general locomotion potential is not affected by size, at least not within the size range of these species.

Concerning different segments of the hind limb, previous studies have not been conclusive in this aspect. For some species, modifications of specific limb segments have been reported and related to locomotor performance (Christian & Garland, 1996; Irschick & Jayne, 2000; Herrel, Meyers & Vanhooydonck, 2002). In our study system, there is evidence for differential growth of different hind limb segments. Although the femur and tibia (FL, TBL) appear to grow proportionally in relation to total hind limb length, this is not true for the hind foot and toe (4TL), which grow disproportionately in both sexes of both species (Fig. 3, Table 5). This disproportionate growth of the distal part of the hind limb may indicate a trade-off between speed and stability because it could be a biomechanical solution for increasing stride length without raising the centre of mass. Interestingly, in other lizard species (i.e. *Anolis*; Irschick, 2002), the length of the toe was the only hind limb element that actually correlated to stride length.

In conclusion, our detailed analysis of sexual and ontogenetic variation of morphological traits relative for locomotion indicates that, although important sexual dimorphism exists both in absolute and relative size of body parts, ontogenetic trajectories vary for different traits and there is some evidence for the existence of morphological constraints. Because of the high relevance of the examined traits for interspecific variation in locomotion related to habitat use and escape from predators (Van Damme *et al.*, 2003; Schulte *et al.*, 2004; Irschick *et al.*, 2005; Vanhooydonck *et al.*, 2007), the described morphological patterns may also have functional influences at the intraspecific level. Future studies should aim to explore sexual differentiation in locomotion. Laboratory tests should be carried out to quantify performance measures (speed, acceleration, etc.) under different conditions and analyse movement gape and kinematics in both sexes, whereas standardized field observations could explore sexual microhabitat segregation and test hypotheses of the potential ecological significance of the observed morphological sexual dimorphism. Additionally, sexual dimorphism in locomotion-related morphological traits may also be under the influence of sexual selection in *Podarcis* because locomotor performance has been associated with male dominance in other lizard species (Garland, Hankins & Huey, 1990; Robson & Miles, 2000; Perry *et al.*, 2004; but see also López & Martín, 2002). Finally, behavioural mechanisms may also be involved in shaping locomotion patterns in both sexes and compensating for morphological constraints (Bauwens *et al.*, 1995). On the other hand, a comparison with other species of *Podarcis*, with more saxicolous habits, and for which detailed data are not currently available, might shed light on the evolutionary processes modifying the characters in question in this group of lizards.

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