Head shape allometry and proximate causes of head sexual dimorphism in *Podarcis* lizards: joining linear and geometric morphometrics

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Podarcis bocagei and *Podarcis carbonelli* are two lacertid species endemic to the western Iberian Peninsula, and both show head size and shape sexual dimorphism. We studied immature and adult head sexual dimorphism and analysed ontogenetic trajectories of head traits with body and head size, aiming to shed light on the proximate mechanisms involved. Immatures were much less dimorphic than adults, but geometric morphometric techniques revealed that head shape sexual differences are already present at this stage. Males and females differed in allometry of all head characters with body size, with males showing a disproportionate increase of head size and dimensions. On the other hand, head dimensions and head shape changed with increasing head size following similar trends in both sexes, possibly indicating developmental restrictions. Consequently, adult sexual dimorphism for head characters in these species is the result of both shape differences in the immature stage and hypermetric growth of the head in relation to body size in males. © 2008 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2008, **93**, 111–124.

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INTRODUCTION

Sexual dimorphism, the morphological differentiation of sexually mature males and females, is a common characteristic of both plants and animals (Darwin, 1874; Andersson, 1994) and is thought to reflect the adaptation of both sexes to their different reproductive roles (Fairbairn, 1997). Sexual size dimorphism (SSD) is common in reptiles (Schoener, 1977; Fitch, 1981; Stamps, 1983). Lizards, in particular, provide the opportunity for comparative studies and are a good model to study the evolution of SSD because this group presents a remarkable variation in both direction and magnitude of SSD (Rutherford, 2004; Cox,

Skelly & John-Alder, 2005). Two primary, not mutually exclusive, hypotheses have been proposed for the evolution of SSD in lizards: (1) sexual selection for large male size, which confers an advantage in intrasexual antagonistic behaviour (Stamps, 1983; Vitt & Cooper, 1985; Hews, 1990; Cox *et al.*, 2005) and (2) natural selection for large female size, related to a fecundity advantage of larger females (Braña, 1996; Olsson *et al.*, 2002). Some studies have also attributed SSD in lizards to sexual niche segregation (Schoener, 1967; Slatkin, 1984; Shine, 1989), but such explanations have been widely contradicted and are thought only to play a subsidiary role in the evolution and maintenance of sexual dimorphism (Andersson, 1994; Braña, 1996; Fairbairn, 1997).

Another important aspect to consider is sexual dimorphism of different body parts. Although total

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size has attracted more attention in sexual dimorphism studies, the relative size and shape of different body parts can be much more informative of the selective pressures posed on each sex (Cooper & Vitt, 1989; Braña, 1996; Hews, 1996; Barbadillo & Bawens, 1997; Butler & Losos, 2002; Olsson *et al.*, 2002; Kratochvil *et al.*, 2003). Sexual size and shape dimorphism are not necessarily interdependent and different species may exhibit different combinations of the two, being dimorphic in both size and shape (Butler & Losos, 2002; Baird *et al.*, 2003; Kaliontzopoulou, Carretero & Llorente, 2007), only shape (Carretero & Llorente, 1993; Herrel *et al.*, 2001b; Schwarzkopf, 2005), or only size (Kratochvil *et al.*, 2003). Because different body parts serve different (and in cases multiple) functions, focusing on particular structures can offer insights to the evolutionary mechanisms underlying sexual dimorphism.

In this context, the lizard head could be a paradigm for mosaic evolution due to the numerous evolutionary forces acting on it. It is involved in a variety of crucial functions, including feeding (Herrel, Van Damme & De Vree, 1996; Herrel *et al.*, 1999a, b; Herrel, de Grauw & Lemos-Espinal, 2001a), territory acquisition and defence (Stamps, 1983; Heulin, 1988), habitat and refuge use (Arnold, 1998a, b), and mating (Hews, 1990; Gvoždík & Van Damme, 2003). All these functions provide opportunities for the action of selective forces on head size and shape that could be operating in the same or in opposite directions. From the point of view of intersexual differentiation, head dimorphism is a common pattern in many lizard families (Agamidae: Thompson & Withers, 2005; Eublepharidae: Kratochvil & Frynta, 2002; Gekkonidae: Saenz & Conner, 1996; Lacertidae: Braña, 1996; Gvoždík & Van Damme, 2003; Bruner *et al.*, 2005; Iguanidae: Cooper & Vitt, 1989; Polychrotidae: Preest, 1994; Scincidae: Bull & Pamula, 1996; Teiidae: Anderson & Vitt, 1990). Males usually have larger and more robust heads than females, a pattern that is thought to be driven by sexual selection (Andersson, 1994; Braña, 1996).

Apart from the evolutionary mechanisms that underlie sexual size and shape dimorphism, the elucidation of its proximate causation has attracted interest (Shine, 1990; Stamps, 1993; Andrews & Stamps, 1994; Watkins, 1996; Cox *et al.*, 2005). Important factors that might influence differences between adults of different sexes include size at birth, duration and rate of growth, survival, and timing of sexual maturity (Stamps, 1983, 1993; Shine, 1990; Haenel & John-Alder, 2002). Taking into account the increasing amount of research dealing with the connection between development and evolution (Klingenberg, 1998), various studies have demonstrated that the understanding of the forces implicated in the evolution of sexual dimorphism depends on an understanding of the allometric patterns and heterochronic processes related to sexual differences (Shine, 1990; Shea, 1992; Stamps, 1993; Hews, 1996; Watkins, 1996; Fairbairn, 1997). A good comprehension of the proximate processes that lead to morphological differentiation of adult males and females can be crucial for the elucidation of the evolutionary pressures, and their timing, that act on each sex.

In a previous study (Kaliontzopoulou *et al.*, 2007), we described patterns of head size and shape sexual dimorphism in adult *Podarcis bocagei* Seoane, 1884 and *Podarcis carbonelli* (Pérez-Mellado, 1981), two Iberian lacertids, and concluded that important sexual differences exist in both species. In the present study, we investigate the proximate causes underlying adult head sexual dimorphism in these species. For this purpose, we apply both linear and geometric morphometrics to explore head size and shape sexual dimorphism in four steps. First, we examine absolute sexual differences in head dimensions and geometric shape in both adults and immatures, to gain insights to the starting and ending points of head ontogenesis in males and females. Second, we examine how absolute head size differences between both sexes are related to total body size; this will allow total body size to be separated from head size and thus answer questions about the direct target and timing of evolutionary mechanisms. Were immature lizards monomorphic for head characters and developmental patterns common in both sexes, sexual selection should be concluded to act on overall body size, rather than head size. If, by contrast, head size and dimensions are directly under selection, we expect to find immature dimorphism and/or different allometric relationships with body size between sexes. Subsequently, we focus on head shape development and investigate how head dimensions vary with head size, aiming to detect specific head features that might exhibit an over-development in one sex independently of total head size. Finally, we use geometric morphometrics to perform a fine-scale analysis of dorsal and lateral head shape development, an approach that will facilitate the study of different head regions and help to detect those that are particularly modified during ontogeny.

MATERIAL AND METHODS
STUDY SPECIES

Podarcis bocagei and *P. carbonelli* are members of the lizard family Lacertidae and are both endemic to the western Iberian Peninsula. They were considered conspecific until recently, but morphological and genetic evidence corroborate the specific status of *P. carbon-*

elli (Sá-Sousa *et al*., 2000; Sá-Sousa, 2001a; Sá-Sousa & Harris, 2002). Although they belong to the same species group, they are not sister taxa and are separated by a considerable genetic distance (Harris & Sá-Sousa, 2001, 2002; Pinho, Ferrand & Harris, 2004, 2006). They are approximately similar morphologically (Sá-Sousa *et al*., 2000; Harris & Sá-Sousa, 2001; Sá-Sousa & Harris, 2002; Kaliontzopoulou, 2004; Kaliontzopoulou, Carretero & Llorente, 2005, 2007) and ecologically, both exhibiting ground-dwelling habits (Pérez-Mellado, 1981, 1997a; Sá-Sousa, 2001a, b; Carretero *et al*., 2002). Both species show a marked sexual dimorphism, with males usually being larger than females and with a more robust habitus. Head sexual dimorphism is also notable in both species, with adult males having not only a bigger head relative to SVL, but also a more robustly built cephalic structure (Kaliontzopoulou *et al*., 2007).

SPECIMENS EXAMINED

Lizards were captured by hand in north-west Portugal from April 2001 to August 2002 in three sites along the Atlantic coastline of Portugal, with similar climatic conditions (Direcção Geral do Ambiente, 1995) and similar habitats corresponding to Atlantic dunes (Barreto-Caldas, Honrado & Paiva, 1999). Specimens of *P. bocagei* were collected from two localities, Mindelo (UTM 29T NF27) and Espinho (UTM 29T NF24, NF34). Specimens of *P. carbonelli* were also collected from the later locality, as well as from Torreira (UTM 29T NF21). The sex and state of sexual maturity of the animals were verified by dissection (Carretero *et al*., 2006).

LINEAR MORPHOMETRICS

For each specimen, we recorded snout–vent length (SVL), head length (HL) from the tip of the snout to the border of the collar, head width (HW) at the widest point and head height (HH) at the highest point. All measurements were taken to the closest 0.01 mm using electronic callipers and variables were log-transformed prior to analyses. To represent total head size, we followed Mosimann's (1970) geometric-mean method on head dimensions and calculated head size (HS) as the third root of the product of HL, HW, and HH.

We applied univariate two-way analysis of variance (ANOVA) on biometric variables of each species separately to investigate the effect of sex, class and their interaction (sex × class) and establish absolute size patterns. Additionally, we examined the allometry between head dimensions and SVL to test whether sexual differences in head dimensions of adults simply reflect sexual differences in body size or relative head size develops under different trajectories in both sexes. Moreover, we examined how head dimensions changed with increasing head size, in search of sex-specific over-development of specific characters. For both purposes, regression analyses were conducted in each sex separately. Because measurement error was present in both the dependent and the independent variables, ordinary least-squares regression would produce skewed values for the regression slopes (McArdle, 1988; Sokal & Rohlf, 1995); therefore, we applied reduced major axis (RMA) regression (Bohonak, 2002). We tested for deviation from isometry following Clarke (1980). Homogeneity of slopes between sexes was evaluated by examination for overlap of the 95% confidence intervals (CI) of the slopes' estimates.

GEOMETRIC MORPHOMETRICS

We took high resolution photographs of the dorsal and lateral view of the head of all specimens using a digital camera mounted on a stand to ensure that the objective were always parallel to the surface examined. We placed graph paper beneath each lizard's head to record scale. For the lateral view, the right side of the head was always recorded. For the purpose of the present study, it was important to capture overall dorsal and lateral head shape at the same time as satisfactorily subdividing the head into regions. Because head scales develop together with underlying regions of the skull (Bellairs & Kamal, 1981), landmarks were defined in scale intersections evenly distributed throughout the dorsal and lateral surface of the head. We recorded 30 and 16 landmarks on the dorsal and lateral view of the head, respectively (Fig. 1), using tpsDig (Rohlf, 2005a). The dorsal surface of the head is structurally symmetrical and we were not interested in analysing asymmetry; therefore, we averaged both sides to avoid effects of lateral asymmetry (Corti & Rohlf, 2001). For this purpose, landmarks 1, 12, 15, 16, 20, and 25 were used as the axis of symmetry and the remaining bilateral landmarks were averaged across the midline. All statistical analyses of the dorsal view were conducted on these half configurations. However, deformation grids are presented for a symmetrical bilateral configuration, to make visualization of shape change easier and to avoid confusing effects of asymmetrical variation along the midline. All shape analyses were carried out using software from the tps series. Spline graphs for comparing groups were produced using Morpheus et al. software (Slice, 1999).

We confirmed that the distances between specimens in the shape space are sufficiently small using tpsSmall (Rohlf, 2003). Subsequently, we used tpsRelw (Rohlf, 2005b) to superimpose all specimens applying
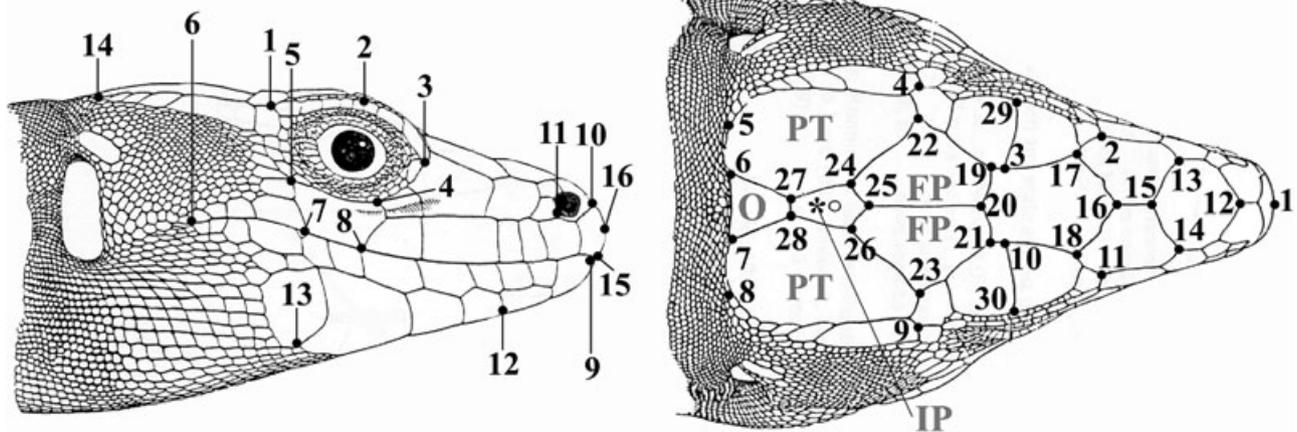
Figure 1. Landmarks recorded on the dorsal and lateral view of the lizards' head. PT, parietals; FP, frontoparietals, IP, interparietal; O, occipital.

a generalized least squares Procrustes superimposition (GPA or GLS; Rohlf & Slice, 1990; Rohlf, 1999), in order to standardize the size, translate, and rotate the landmark configurations. Using the same software, we extracted partial warp scores (including the uniform component), which were used as shape variables. To depict differences between groups, quantify sexual dimorphism in the immature and adult stage, and evaluate the degree of ontogenetic shape change in each sex, we calculated Generalized Procrustes Distances (GPD) between groups' means. To test for significance of the observed distances, we randomly assigned specimens to groups and recalculated the distances. The significance level of the observed distances was then estimated as the proportion of random distances (out of 999 replicates) that was greater than the observed distance (Adams & Rohlf, 2000; Adams, 2004). The same procedure was used to compare distances between different pairs. Because multiple comparisons were carried out on the same data (Curran-Everett, 2000), *P*-values for each species were adjusted following the False Discovery Rate procedure (Benjamini & Hochberg, 1995).

To compare fine patterns of head shape ontogeny in the two sexes, we conducted regression analyses. For this purpose, we used the logarithm of centroid size (CS) of landmark coordinates to represent head size. CS is the quantity standardized for in Procrustes Analysis and is uncorrelated to shape variables in the absence of allometry (Bookstein, 1991; Dryden & Mardia, 1998; Zelditch *et al.*, 2004). Therefore, significant results in the multivariate regression of shape on CS indicate an allometric effect of size on shape. We carried out a multivariate regression of shape variables on LOG (CS) in tpsRegr (Rohlf, 2004) to test the assumption of isometry between shape and size. We analysed the ontogenetic trajectories of head

shape on centroid size for each sex separately and tested for common slopes and intercepts.

RESULTS

LINEAR MORPHOMETRICS

ANOVA comparisons on head dimensions confirmed that both species were dimorphic in the adult stage, but monomorphic when immature. The same was true for SVL in *P. bocagei*, but the effect of sex was not significant for SVL in *P. carbonelli*. However, the interaction term class × sex was found significant (Table 1), indicating that the degree of total size sexual dimorphism changes between ontogenetic stages. For both species, adult males were bigger than adult females for all the variables analysed. No significant sexual differences where detected between immatures of either species for any of the biometric variables. Obviously, adults were bigger than immatures for all the characters examined regardless of the sex or species (Table 1).

Analyses of allometry of head dimensions with SVL showed that males and females of both species differ significantly in their growth trajectories. A comparison of the 95% CI of RMA slopes of head characters on SVL showed that slope estimates were always higher for males than for females (Table 2). Moreover, males of both species showed a positive allometry of HH and HS (Fig. 2), whereas the remaining the characters were isometric or hypometric for both sexes.

On the other hand, analyses of the relationship between head dimensions and HS revealed patterns common for both sexes; although, in some cases, tests for deviation from isometry yielded different results for males and females of each species, RMA slopes of both sexes were not statistically distinguishable, 95% CI of slope estimates always overlapping. It is interesting to

Table 1. Descriptive statistics of biometric variables (log-transformed) for immature and adult males and females of both species studied

	Podarcis bocagei (d.f. = 1, 245)					
	Immature females (N = 30)	Immature males (N = 50)	Adult females (N = 72)	Adult males (N = 97)	F	P-value
Log (SVL)	1.55 ± 0.06 1.38–1.65	1.55 ± 0.09 1.32–1.70	1.72 ± 0.03 1.65–1.81	1.76 ± 0.03 1.67–1.81	4.61 676.97 5.99	0.03 0.00 0.02
Log (HL)	1.08 ± 0.05 0.93–1.16	1.10 ± 0.08 1.88–1.23	1.22 ± 0.03 1.16–1.28	1.31 ± 0.03 1.22–1.36	63.21 689.44 20.17	6.82×10^{-14} 0.00 1.09×10^{-5}
Log (HW)	0.72 ± 0.05 0.57–0.80	0.75 ± 0.07 0.59–0.87	0.86 ± 0.03 0.79–0.91	0.95 ± 0.03 0.87–1.02	92.85 658.01 28.58	0.00 0.00 2.05×10^{-7}
Log (HH)	0.53 ± 0.06 0.37–0.65	0.55 ± 0.10 0.32–0.76	0.71 ± 0.04 0.62–0.80	0.83 ± 0.05 0.69–0.92	61.22 687.61 26.39	1.52×10^{-13} 0.00 5.68×10^{-7}
Log (HS)	0.78 ± 0.06 0.62–0.86	0.80 ± 0.08 0.60–0.95	0.93 ± 0.03 0.87–0.97	1.03 ± 0.04 0.94–1.10	76.93 740.76 27.29	3.33×10^{-16} 0.00 3.74×10^{-7}
	Podarcis carbonelli (d.f. = 1, 252)					
	Immature females (N = 36)	Immature males (N = 25)	Adult females (N = 90)	Adult males (N = 105)	F	P-value
Log (SVL)	1.54 ± 0.06 1.39–1.63	1.53 ± 0.05 1.40–1.60	1.68 ± 0.03 1.61–1.76	1.70 ± 0.04 1.59–1.78	0.04 582.93 4.45	0.84 0.00 0.04
Log (HL)	1.07 ± 0.06 0.95–1.15	1.09 ± 0.05 0.98–1.15	1.18 ± 0.03 1.12–1.27	1.25 ± 0.04 1.14–1.35	46.26 526.47 13.48	7.47×10^{-11} 0.00 2.94×10^{-4}
Log (HW)	0.71 ± 0.05 0.61–0.83	0.73 ± 0.05 0.61–0.80	0.81 ± 0.03 0.76–0.89	0.89 ± 0.04 0.78–0.99	73.42 481.53 17.67	1.11×10^{-15} 0.00 3.66×10^{-5}
Log (HH)	0.52 ± 0.06 0.37–0.63	0.53 ± 0.08 0.39–0.66	0.68 ± 0.04 0.54–0.77	0.76 ± 0.07 0.59–0.89	25.46 445.36 17.87	8.66×10^{-7} 0.00 3.31×10^{-5}
Log (HS)	0.77 ± 0.06 0.64–0.85	0.78 ± 0.05 0.67–0.86	0.89 ± 0.03 0.81–0.97	0.97 ± 0.05 0.85–1.07	48.36 540.99 18.65	3.04×10^{-11} 0.00 2.26×10^{-5}

Values are the mean ± standard deviation (SD) (top) and range (bottom). F- and P-values are presented for analysis of variance comparisons considering sex (top), class (middle) and their interaction (bottom). SVL, snout–vent length; HL, head length; HW, head width; HH, head height; HS, head size.

note that HH was always hypermetric in relation to HS for both species and sexes (Table 3, Fig. 2).

GEOMETRIC MORPHOMETRICS

The examination of GPD between different groups gave significant results in most cases, indicating shape differences between sexes and classes (Table 4). Dorsal and lateral head shape differed significantly between sexes, both for adults and immatures, with the sole exception of immature *P. carbonelli*, which did not show significant sexual differences. Dorsal and lateral head shape differed significantly between ontogenetic classes within

Table 2. Estimated parameters and confidence intervals for the reduced major axis regression of head characters on snout–vent length

	Intercept (95% CI)	Slope (95% CI)	R^2	P (isometry)
Podarcis bocagei females ($N = 102$)				
HL	−0.21 (−0.26 to −0.16)	0.83 (0.80–0.86)	0.97	3.20×10^{-5} (−)
HW	−0.50 (−0.57 to −0.43)	0.79 (0.75–0.83)	0.93	1.53×10^{-4} (−)
HH	−1.11 (−1.20 to −1.02)	1.06 (1.00–1.11)	0.93	0.355
HS	−0.59 (−0.63 to −0.54)	0.88 (0.86–0.91)	0.97	1.30×10^{-3} (−)
Podarcis bocagei males ($N = 147$)				
HL	−0.40 (−0.43 to −0.37)	0.97 (0.95–0.99)	0.99	0.119
HW	−0.71 (−0.76 to −0.66)	0.94 (0.92–0.97)	0.97	0.092
HH	−1.46 (−1.53 to −1.38)	1.30 (1.25–1.35)	0.96	0 (+)
HS	−0.84 (−0.88 to −0.80)	1.06 (1.04–1.08)	0.99	0.011 (+)
Podarcis carbonelli females ($N = 126$)				
HL	−0.24 (−0.29 to −0.19)	0.85 (0.82–0.88)	0.96	1.75×10^{-4} (−)
HW	−0.48 (−0.55 to −0.42)	0.77 (0.73–0.81)	0.91	4.90×10^{-5} (−)
HH	−1.23 (−1.34 to −1.13)	1.14 (1.07–1.20)	0.90	0.055
HS	−0.62 (−0.66 to −0.57)	0.90 (0.87–0.92)	0.97	3.65×10^{-3} (−)
Podarcis carbonelli males ($N = 130$)				
HL	−0.40 (−0.45 to −0.35)	0.97 (0.94–1.00)	0.97	0.431
HW	−0.70 (−0.78 to −0.63)	0.94 (0.90–0.98)	0.93	0.244
HH	−1.66 (−1.77 to −1.55)	1.43 (1.36–1.49)	0.93	0 (+)
HS	−0.89 (−0.94 to −0.84)	1.09 (1.06–1.13)	0.97	7.05×10^{-3} (+)

P (isometry) indicates the result of a test for isometry (−): slopes significantly smaller than 1 (+): slopes significantly greater than 1. 95% CI, 95% confidence interval; HL, head length; HW, head width; HH, head height; HS, head size.

each sex of both species. Males and females of both species were more similar as immatures than as adults, both for the dorsal and the lateral configuration of landmarks. Similarly, males always went through a more intense shape change along their growth trajectory, GPD between male immatures and adults being higher than those observed for the respective females (Table 4).

Ontogenetic shape change, analysed through examination of deformation grids, was similar in both

species. Examination of the dorsal and lateral landmark configurations revealed that shape differences between immatures and adults are primarily related to the posterior region of the head (Fig. 3). Dorsally, the posterior part of the pileus, including the fronto-parietal, parietal, interparietal, and occipital scales, is the region that appears more deformed. Laterally, shape differences between the two ontogenetic stages are due to deformation of the tympanic area of the head. Note that, both for the dorsal and the lateral
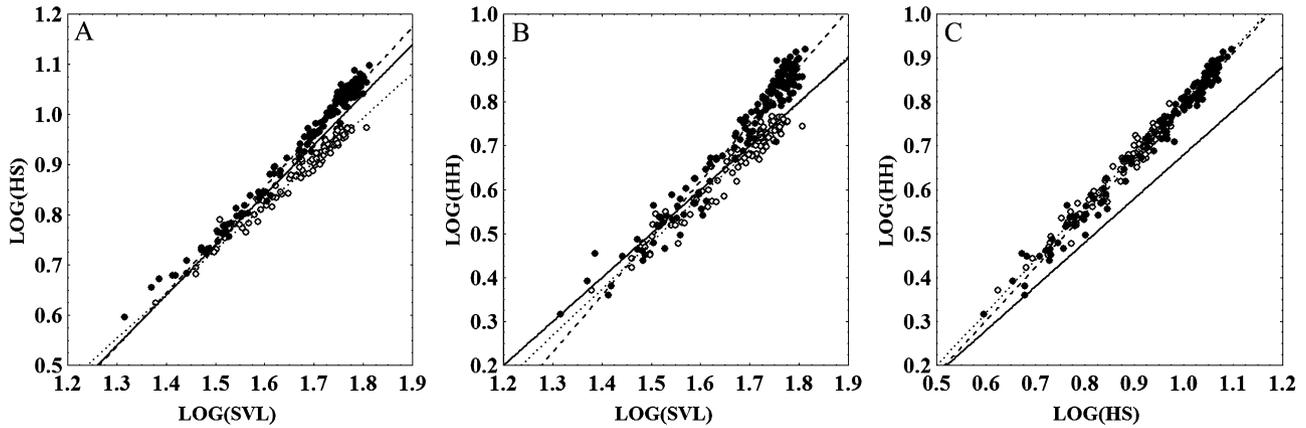
Figure 2. Relationship of head height (HH) and head size (HS) with snout–vent length (SVL) (A, B, respectively) and HH with HS (C) in males (closed circles, dashed line) and females (open circles, dotted line) of *Podarcis bocagei* estimated by reduced major axis regression (patterns were similar for *Podarcis carbonelli*). The continuous line represents isometry.

Table 3. Estimated parameters and confidence intervals for the reduced major axis regression of head dimensions on head size

N	Intercept (95% CI)	Slope (95% CI)	R^2	P (isometry)
Podarcis bocagei females (N = 102)				
HL	0.34 (0.32 to 0.36)	0.95 (0.92–0.97)	0.99	0.060
HW	0.02 (−0.01 to 0.05)	0.90 (0.86–0.93)	0.96	0.017 (−)
HH	−0.40 (−0.44 to −0.37)	1.20 (1.16–1.24)	0.97	3.50×10^{-5} (+)
Podarcis bocagei males (N = 147)				
HL	0.37 (0.35 to 0.38)	0.91 (0.90–0.93)	0.99	1.20×10^{-5} (−)
HW	0.04 (0.02 to 0.06)	0.89 (0.87–0.91)	0.98	4.70×10^{-5} (−)
HH	−0.43 (−0.46 to −0.41)	1.22 (1.20–1.25)	0.98	0 (+)
Podarcis carbonelli females (N = 126)				
HL	0.34 (0.31 to 0.36)	0.95 (0.92–0.98)	0.97	0.124
HW	0.05 (0.01 to 0.08)	0.86 (0.82–0.90)	0.93	0.007 (−)
HH	−0.45 (−0.50 to −0.41)	1.27 (1.22–1.32)	0.95	2×10^{-6} (+)
Podarcis carbonelli males (N = 130)				
HL	0.39 (0.37 to 0.41)	0.89 (0.87–0.93)	0.98	3.8×10^{-5} (−)
HW	0.06 (0.03 to 0.09)	0.86 (0.82–0.89)	0.95	0.002 (−)
HH	−0.50 (−0.53 to −0.46)	1.30 (1.26–1.35)	0.97	0 (+)

P (isometry) indicates the result of a test for isometry (−): slopes significantly smaller than 1 (+): slopes significantly greater than 1. HL, head length; HW, head width; HH, head height.

Table 4. Generalized Procrustes Distances (GPD) between sexes and classes of the two species studied for the dorsal and lateral head shape variables

	Dorsal				
	Immatures		Adults		
Between sexes	GPD	*P*	GPD	*P*	*p*-dist
Podarcis bocagei	0.010	0.049	0.020	0.001	0.001
Podarcis carbonelli	0.010	0.324	0.015	0.002	0.002
	Females		Males		
Between classes	GPD	*P*	GPD	*P*	*p*-dist
Podarcis bocagei	0.031	0.001	0.041	0.001	0.001
Podarcis carbonelli	0.024	0.002	0.036	0.002	0.003
	Lateral				
	Immatures		Adults		
Between sexes	GPD	*P*	GPD	*P*	*p*-dist
Podarcis bocagei	0.027	0.001	0.024	0.001	0.364
Podarcis carbonelli	0.020	0.095	0.026	0.002	0.004
	Females		Males		
Between classes	GPD	*P*	GPD	*P*	*p*-dist
Podarcis bocagei	0.053	0.001	0.075	0.001	0.001
Podarcis carbonelli	0.059	0.002	0.075	0.002	0.008

P-values for the distances (p) were calculated using a resampling procedure (see Material and methods). *p*-dist: significance level evaluated by resampling for the difference of distances between groups. *P*-values are presented after adjustment using the False Discovery Rate procedure.
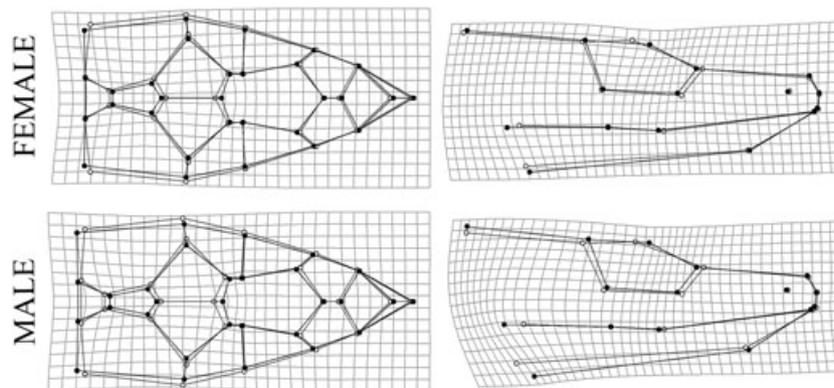
Figure 3. Deformation grids showing ontogenetic shape change for the dorsal (left) and the lateral (right) side of the head for females (top) and males (bottom). Open circles represent immatures and closed circles represent adults. Grids are presented only for *Podarcis bocagei*, but patterns are similar for both species.

configurations of landmarks, deformation patterns are similar between sexes, but shape change is more intense in males, represented by more deformed grids between immature and adult landmark configurations (Fig. 3).

Multivariate regressions between the geometric shape variables and centroid size gave significant correlations in all the groups examined, indicating an allometric relationship between head size and shape. The tests for homogeneity of slopes and intercepts between sexes gave similar results for both species. For the dorsal configuration of landmarks, the tests conducted in tpsRegr indicated that both sexes follow trajectories with similar slopes (*P. bocagei*: Wilks' lambda = 0.792, d.f. = 64, 350, $P = 0.971$; *P. carbonelli*: Wilks' lambda = 0.729, d.f. = 64, 384, $P = 0.429$), but different intercepts (*P. bocagei*: Wilks' lambda = 0.489, d.f. = 32, 177, $P = 7.08 \times 10^{-15}$;   *P. carbonelli*:   Wilks' lambda = 0.481, d.f. = 32, 194, $P = 1.45 \times 10^{-17}$). For the lateral configuration, males and females of *P. bocagei* also follow trajectories with similar slopes (Wilks' lambda = 0.728, d.f. = 56, 404, $P = 0.124$) but different intercepts (Wilks' lambda = 0.529, d.f. = 28, 204, $P = 1.99 \times 10^{-16}$). Surprisingly, results were different for the lateral configuration of *P. carbonelli*, for which male and female trajectories were found to differ both in slope (Wilks' lambda = 0.706, d.f. = 56, 414, $P = 0.035$) and intercept (Wilks' lambda = 0.568, d.f. = 28, 209, $P = 3.10 \times 10^{-14}$).

DISCUSSION

The analysis of dimorphism in immatures and head ontogeny is of great interest for elucidating the mechanisms underlying adult sexual dimorphism in these two species. As in many lizards, adult males of *P. bocagei* and *P. carbonelli* have larger heads than adult females, both in absolute and relative terms. On the other hand, immatures of both species are monomorphic in head size and relative dimensions, but not in shape. This does not constitute a discrepancy. Geometric morphometrics are expected to have a higher sensitivity and detect finer differences because a much higher number of variables are evaluated. Although immature lizards are usually reported to be monomorphic (Cooper & Vitt, 1989; Andrews & Stamps, 1994; Watkins, 1996), in the present study, we found evidence that some sexual differences in head shape already exist in the immature stage. This supports the hypothesis of selection acting on head shape; head sexual differentiation starts early during ontogeny and dimorphism of immature lizards provides strong evidence that head sexual dimorphism is not just the result of bigger male head size and/or other (i.e. developmental, demographic) factors (Stamps, 1993).

SEXUAL SELECTION ON RELATIVE HEAD SIZE

Linear morphometrics revealed divergent head growth trajectories between the sexes in both species examined. Males always show higher RMA slopes than females for all the head characters in relation to body size (SVL). Additionally, head size (HS) and height (HH) are hypermetric in relation to body size in males but not in females, clearly indicating that males allocate more effort than females to head increase relative to total body size. This pattern is common in the Lacertidae and it has been related to sexual selection mechanisms (Braña, 1996; but see also Kratochvil *et al.*, 2003). It has been repeatedly shown that relative head size, head dimensions, and especially head height are directly related to bite performance and force (Herrel *et al.*, 1996, 1999a, b, 2001a), but also to male dominance (Carpenter, 1995; Husack *et al.*, 2006). Such selective pressures could be related to antagonistic behaviour between males for territory defence and/or mate acquisition, in which individuals with bigger heads would have an advantage. Moreover, a bigger head could be advantageous for male lacertids during copulation because males have to grab females and immobilize them in order to copulate with them (Verbeek, 1972; Heulin, 1988; Hews, 1990; Herrel *et al.*, 2001b; Gvoždík & Van Damme, 2003). However, these hypotheses still need to be tested in the species in question because no direct data on male territorial behaviour and reproductive success in relation to morphology are available for *Podarcis* lizards.

MODIFICATION OF HEAD DIMENSIONS WITH INCREASING HEAD SIZE

Although it is evident that head size relative to body size is under sexual selection in male *Podarcis* studied, the question still remains as to whether particular dimensions of the head are especially modified during head development. The analysis of head dimensions in relation to head size revealed common patterns for both sexes. Although there is an apparent inconsistency between the results for deviation from isometry and comparison of RMA slopes between sexes, this is probably due to excessive strictness of tests for deviation from isometry (demonstrated by not significant *P*-values in cases where slope confidence intervals lie below 1; Table 3). Because RMA slope estimates of males and females are not statistically distinguishable, we must conclude that head dimensions develop with increasing head size following similar trends in both sexes, indicating that total head size in relation to body size is the main character being differentiated in male *Podarcis*.

Hypermetry of head height in relation to SVL in males (Table 2, Fig. 2) is a result of hypermetric head size increase, whereas such a hypermetry is not demonstrated in females due to smaller head size. Whether head size or head height is the direct target of sexual selection cannot be distinguished at present; however, it appears that head height is inevitably modified as head size increases and the commonality of head dimensions–HS trajectories between sexes could be the result of anatomical and structural restrictions constraining cranium growth or genetic correlations between sexes (Lande, 1980; Rice & Chippindale, 2001). Although few studies have dealt with the cranial development of *Podarcis* species, Barahona & Barbadillo (1998) found no sexual differences in the cranial development of several species of the genus, perhaps indicating that an ontogenetic constraint exists between both sexes. However, it is important to note that both *P. bocagei* and *P. carbonelli* are ground-dwelling lizards, and therefore are free of constraints on head height due to habitat and refuge use. It has been repeatedly stated that cranial evolution in lizards is linked to their ecological preferences (Arnold, 1998a; Stayton, 2005). It would therefore be interesting to test whether the same pattern is observed in other closely-related species of the *Podarcis hispanica* species complex (Harris & Sá-Sousa, 2002), which are expected to be more constrained in this aspect because they are more saxicolous (Pérez-Mellado, 1997b).

GEOMETRIC SHAPE AND SIZE OF THE HEAD

The results obtained from regression analyses between head size and shape variables are in consistency with the results on modification of head dimensions with head size increase. Again, it is evident that shape is tightly linked to size, which is not surprising because organismal size transformations cannot arise without consequent shape transformations (Thompson, 1917; Sprent, 1972; Brown, West & Enquist, 2000; Zelditch *et al.*, 2004). Regression analyses showed that head shape allometry follows similar allometric slopes in male and female *Podarcis*, probably pointing to some developmental mechanism common to both sexes. The exception of the lateral head shape of *P. carbonelli* should probably be attributed to an effect of sample size or statistical comparisons. In both males and females, bigger cephalic structures are characterized by a more developed posterior head region (Fig. 3), a pattern that has been described for other lizard species (Monteiro & Abe, 1997; Bruner *et al.*, 2005; Vidal *et al.*, 2005). Moreover, this model is congruent with the patterns of cranial development in lacertids because the posterior region of the skull and in particular the parietal region is the last to be ossified and continues developing until advanced stages in the lizards' growth trajectory (Bellairs & Kamal, 1981; Barahona & Barbadillo, 1998).

Although analysis of the external morphology is not sufficient to determine the evolutionary advantages obtained by head shape transformation in males, some hypotheses could be formulated based on previous knowledge of the functional anatomy of the cranium in lacertid lizards. Hypermetry of head size and height and overdevelopment of the tympanic area of the head could be a result of sexual selection pressures acting on male bite force, further reinforcing the advantages obtained by bigger head size relative to SVL. As mentioned previously, increased bite force is advantageous for male lizards both in male–male combats and copulation with females (Carpenter, 1995; Herrel *et al.*, 1996, 2001b; Husack *et al.*, 2006). Increased head height could provide more space for the mandible adductor muscles, but also confers other advantages for bite performance because it allows the jaw muscles to insert more perpendicularly at the lower jaw and increase the power transmitted to the quadrato-articular joint (Haas, 1973). Relative to the deformation of the tympanic area, this might also be the result of specific modifications (volume and orientation) of the jaw adductors in males. In other lizard families, the morphology of the jaw adductor might be modified without head size increase (Xenosauridae: Herrel *et al.*, 2001a). However, only detailed studies of the functional anatomy of the head in male and female members of the two species could directly confirm these hypotheses.

In conclusion, the results obtained by linear and geometric morphometrics indicate that not only is head size overdeveloped relative to body size in male *P. bocagei* and *P. carbonelli*, but also sexual differences in head shape are present independently of size. In both species, some of the results indicate developmental constraints common to both sexes, which condition the modification of head dimensions and shape when head size increases and might prevent each sex from reaching its morphological optimum. Geometric morphometric techniques revealed that immatures are already dimorphic before attaining adult size, a fact that would not be surprising under the hypothesis of sexual selection. If head size and shape are crucial for the reproductive performance of males, these characters should already be developed when males reach sexual maturity. Because such a complex structure cannot be acquired instantaneously, it is expected that it should start developing early in the life of a male to give small males any (even if reduced) reproductive chance. Nonetheless, other reproductive strategies

not involving fighting, such as sneaking (Diaz, 1993; López & Martín, 2001) or display behaviour (Molina-Borja, 1981, 1987), should be more frequently used in such circumstances.

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