Evol Ecol
DOI 10.1007/s10682-011-9538-y

ORIGINAL PAPER

Relationships between head morphology, bite performance and ecology in two species of *Podarcis* wall lizards

**Antigoni Kaliontzopoulou · Dean C. Adams · Arie van der Meijden ·
Ana Perera · Miguel A. Carretero**

Received: 19 July 2011 / Accepted: 3 November 2011

Abstract Understanding the relationship between form and function is central to our comprehension of how phenotypic diversity evolves. Traits involved in multiple activities, such as social interactions and ecological resource use, are under the influence of different evolutionary forces potentially acting in opposite directions. Such systems provide the opportunity of understanding how potential constraints on morphological variation may influence whole-organism performance. In this study we examined morphology and bite performance in two closely related species of *Podarcis* wall lizards with divergent microhabitat preferences, to investigate how natural and sexual selection interact to shape the evolution of head traits. Our results show that although head morphology is markedly different between species and sexes, only sexes differ in bite force, indicating that the ecological differentiation between species is reflected in their morphology but does not constrain performance. Rather, the modification of the relative size of head components between species and a shift in the form-function relationship provide a potential explanation of how equal performance is attained by different morphological configurations. Geometric morphometrics provide a clear, biomechanically meaningful image of how this is achieved and show a bisexual pattern of head shape-bite force association in both species. This, together with a strong allometry of head size on body size and head shape on head size, provides indirect morphological evidence for the importance of sexual selection in shaping morphological and functional patterns. Finally, our findings suggest that the differences observed between species and sexes in head traits and bite performance are not reflected in their dietary ecology, implying that if trophic niche segregation between

---

A. Kaliontzopoulou (✉) · A. van der Meijden · A. Perera · M. A. Carretero
CIBIO/UP, Centro de Investigação em Biodiversidade e Recursos Genéticos, Campus Agrario de Vairão, 4485-661 Vairão, Portugal
e-mail: antigoni@mail.icav.up.pt

A. Kaliontzopoulou · D. C. Adams
Department of Ecology, Evolution, and Organismal Biology, Iowa State University,
Ames, IA 50011, USA

D. C. Adams
Department of Statistics, Iowa State University, Ames, IA 50011, USA

groups occurs, the reasons behind it are not primarily related to head morphology and functional variation.

Keywords Head shape · Geometric morphometrics · Sexual dimorphism · Allometry · Performance

Introduction

The relationship between morphology, performance and ecology is central to our understanding of the evolutionary and ecological processes that drive phenotypic evolution (Wainwright 2007). External morphology is the result of the amalgamation of historical factors, natural and sexual selection, but also proximate factors such as physiology, body condition and growth. Nevertheless, it is widely recognised that performance, rather than morphology, is most frequently the target of selection (Wainwright 2007; Irschick et al. 2008). This means that performance traits, and their association to morphology and ecology, are of cornerstone importance for determining the role and relative contribution of the aforementioned processes in shaping the morphological variation observed in any organismal system (Arnold 1983; Kingsolver and Huey 2003).

Head morphology of lizards and its relation to bite performance and ecology has been a major model system for investigating the integration of different phenotypic components. In many lizard species, the head is involved in multiple and highly relevant ecological and social activities, including feeding, refuge use, mating and male aggressive interactions. Indeed, sexual dimorphism in head size and shape is prominent in many species (Cooper and Vitt 1989; Preest 1994; Braña 1996; Kratochvíl and Frynta 2002; Kaliontzopoulou et al. 2008), a pattern that has been attributed to sexual selection enhancing male potential for antagonism and territoriality (Stamps 1983; Andersson 1994; Braña 1996; Huyghe et al. 2005). This selective mechanism has been shown to act through influences on bite force (Lappin and Husak 2005; Lappin et al. 2006, Husak et al. 2006a; Lailvaux and Irschick 2007; Husak et al. 2009; Herrel et al. 2010). Further, both head morphology and bite force are highly relevant for feeding (Herrel et al. 1998a, 2001d; Metzger and Herrel 2005; Vincent and Herrel 2007), suggesting that natural selection can also play a role in head shape and bite performance diversification. Additionally, head dimensions are directly associated with microhabitat and refuge use (Arnold 1998) and both head size and shape have been shown to be under the influence of natural selection (Vitt et al. 1997; Vanhooydonck and Van Damme 1999; Herrel et al. 2001b; Kaliontzopoulou et al. 2010), under the selective influence of predation. All the above processes act simultaneously, potentially in opposite directions, and different equilibria between them may cause variation in morphology and performance both within and among lizard species.

In the same context, several studies have shown that sexual and natural selection may interact in complex ways, the outcome being variation in the degree of sexual dimorphism in morphological traits across environmental conditions or species (Butler and Losos 2002; Losos et al. 2003; Butler et al. 2007; Stuart-Fox and Moussalli 2007; Kaliontzopoulou et al. 2010). However, the consequences of such interactions for performance have not been investigated in detail. As different functional demands cannot always be simultaneously optimized for the same trait (Perrin and Travis 1992; Walker 2007), the existence of counteracting forces may lead to varying outcomes, depending on the relative force of sexual and natural selection, the traits targeted by the selective mechanisms involved and the strength of dependence among phenotypic traits. For instance, if the optimisation of bite performance under the influence of sexual selection is crucial and morphology-performance relationships are relatively flexible, different head morphologies may accommodate similar bite–force outcomes through the modification of head proportions, internal head anatomy or physiology. In turn, if ecological adaptation to habitat type poses a powerful constraint on head morphology, bite performance may also be constrained as a consequence. Systems where ecological components and/or social interactions are known to vary are ideal for investigating how these different forces interact to shape the evolution of head morphology, bite performance and the relationship between them.

Several previous studies have analysed the effects of body size, head size and head shape on bite performance in lizards (Herrel et al. 2001a; Verwaijen et al. 2002; Herrel and O'Reilly 2006; Lappin et al. 2006; Huyghe et al. 2009; Measey et al. 2009; among others). These studies have shown that, while general rules apply, extensive variation also exists, with different morphological variables being more relevant for bite performance in different groups (see for example Herrel et al. 2001a; Lappin and Husak 2005). This is not unexpected, since bite performance is influenced by several components. The inlever-outlever proportions of the jaw, the size, insertion points and orientation of the jaw musculature and the micro-structure of muscle fibers jointly determine bite force production (Herrel et al. 1998a, b, 2001c). External head morphology is an easily accessible proxy of the combined action of all the above structural components. However, with such diverse factors involved, making sure to record the most relevant morphological parameters can be a challenge and an integrated quantification of morphology is urged. This can be achieved using geometric morphometric (GM) methods, which provide a powerful statistical framework for the analysis of organismal shape while preserving the geometric properties of the studied structures (Bookstein 1991; Adams et al. 2004; Slice 2005). These tools have been increasingly used to study the morphology of complex structures, including lizard head shape (Bruner and Constantini 2007; Kaliontzopoulou et al. 2007, 2008, 2010; Ljubisavljević et al. 2010; Raia et al. 2010; among others). GM methods have also been used successfully to capture biomechanically-relevant shape (Adams and Rohlf 2000; Adams 2004; Rivera 2008; Young et al. 2010), but have not yet been used to investigate lizard head morphology in relation to bite performance.

In this study, we examined head morphology, bite performance and diet in two species of *Podarcis* wall lizards from the Iberian Peninsula with different habitat preferences, to investigate how different evolutionary forces on morphology and performance interact to shape head trait evolution. For the first time, we used both linear and geometric morphometrics to capture variation in head morphology and associate it to bite performance and ecology. Specifically, we aimed at answering the following questions: (1) Are species and sexes morphologically and functionally differentiated, as we expect based on previous knowledge about the action of sexual and natural selection on head traits? (2) If so, which are the morphological traits most highly associated with bite-force variation? (3) Are relationships between head morphology (size and shape) and bite performance uniform across species and sexes? (4) Do species and sexes use different dietary resources? Based on previous studies, we expected to observe the typical patterns of sexual dimorphism (enlarged head traits and higher bite force in males) and the typical morphological differentiation between species inhabiting divergent microhabitats (saxicolous lizards should be flatter). We anticipated that the use of GM methods would further augment our understanding of morphology-performance dimorphism in these lizards; if head shape is modified in males under the influence of sexual selection to enhance bite performance, we expect variation in head shape in males to be correlated with variation in bite force, while such a relationship should be lacking in females. Our comparison between species and sexes also provides evidence on the relative importance of sexual versus natural selection in this phenotypic system. If the influence of natural selection on morphology dominates, we predict that the flat, saxicolous *P. hispanica* type 1A males may show decreased bite performance as compared to the ground-dwelling *P. bocagei* males. In turn, if the influence of sexual selection for increasing bite force in males prevails, we may observe a shift in morphology-performance across species, as a means to maintain important functionality (bite force) under the different head configurations dictated by microhabitat use. Finally, given the importance of head morphology and bite performance for feeding, species and sexes may also use different dietary resources, dietary divergence constituting an additional mechanism that maintains morphological and performance differentiation in this system.

Materials and methods

Study organisms

We focused on two species of wall lizards, *Podarcis bocagei* Seoane, 1884 and *P. hispanica* (Steindachner 1870) type 1A (sensu Harris and Sá-Sousa 2002). These two species present a particularly interesting system for studying morphology-function-ecology relationships, due to their largely shared evolutionary history and geographical distribution as well as their ecological differentiation. They are sister taxa, both being members of the *P. hispanica* species complex (Pinho et al. 2006; Kaliontzopoulou et al. 2011). Additionally, they share a large portion of their geographic distributions (Kaliontzopoulou et al. 2011) and are frequently found in strict syntopy, where similar ecological resources are available to both (Carretero 2008). However, they are quite distinct ecologically: *P. bocagei* is primarily ground-dwelling, but also inhabits human-constructed walls (Kaliontzopoulou et al. 2010), while *P. hispanica* type 1A is primarily saxicolous, being more restricted to big rock outcrops and frequently climbing perpendicular surfaces (Sá-Sousa et al. 2002). Our study was conducted in one of these sympatric sites, found on a coastal location in northern Portugal (Moledo: 41°50.314′N, 8°41.839′W). In this site, both species are principally found on agricultural walls, where they share large part of their microhabitat. We visited the study site in June 2009 and collected a total of 32 male and 29 female *P. bocagei* and 33 male and 30 female *P. hispanica* type 1A adult individuals. At the moment of capture, fecal pellets were obtained from all individuals and preserved in 70% alcohol for diet composition analysis. All lizards were then taken to the laboratory and housed there for 3 days in order to conduct bite force measurements and to quantify morphology. Lizards were housed in a single, 1 m × 1 m terrarium, with natural substrate. The terrarium was kept under natural light-cycle conditions and provided with access to direct sunlight for at least 8 h per day (including the hours during which all bite-measurements took place, see below). After performance experiments (see below) all animals were released back to their location of capture.

Quantified parameters

To quantify morphological variation relevant to bite force and prey consumption we measured four head characters to the closest 0.01 mm using electronic calipers: head length (HL), from the tip of the snout to the posterior border of the collar, head width (HW) at the widest point of the head, head height (HH) at the highest point and mouth opening

(MO), from the tip of the snout to the posterior border of the last supralabial scale (Fig. 1). We also measured snout-vent length (SVL) to represent total body size. All linear variables were log-transformed prior to analyses. Additionally, we obtained high resolution photographs of the right side of the head to study lateral head shape and used tpsDig software (Rohlf 2005) to digitize 12 landmarks (Fig. 1) on the head of each specimen. We then used geometric morphometric approaches (Rohlf and Marcus 1993; Adams et al. 2004) to compare patterns in head shape. First, we performed a Generalized Procrustes Analysis (GPA: Rohlf and Slice 1990) to superimpose all specimens to a common location, and remove the effects of size, location and orientation from the landmark coordinates. We then obtained partial warp scores and uniform shape components (using tpsRelW: Rohlf 2008), which were treated as a set of shape variables for subsequent statistical analyses.

Bite force was measured using an isometric Kistler force transducer (type 9203, Kistler Inc., Winterthur, Switzerland) mounted on a vertical holder and connected to a Kistler charge amplifier (type 5058A, Kistler Inc., Winterthur, Switzerland). Bite force measurements were obtained by provoking the lizards to bite a pair of thin metal plates connected to the force transducer (see Herrel et al. 2001d for a detailed description). The tip of the metal plates where the lizards bit was delimited with a marker to ensure all lizards bit at an equal distance from the revolving arms and thus standardize the point of force exertion. Each lizard was tested five times to ensure that the maximal individual bite force per individual was registered. Before performing bite tests, lizards were allowed to thermoregulate under direct natural sunlight and in a room temperature of about 25°C to ensure that activity body temperatures were attained. The maximum bite force measure per individual was retained and log-transformed for further analyses.

We characterized diet composition for each individual by examining preserved fecal pellets through a binocular dissecting microscope. Prey items were identified to the taxonomic level of Order (all observed prey were arthropods, see "Results"), with the exception of Formicidae, which was considered separately from other Hymenoptera due to their non-flying, aggregated nature. Prey counts were based on cephalic capsules, wings and legs, following the minimum numbers criterion per sample (Carretero 2004). The length and width of intact arthropod body structures (Coleoptera elytra, Hymenoptera and Diptera wings and Homoptera and Heteroptera hemielytra) were measured to the nearest 0.5 mm, which served as a proxy for the size of the consumed prey items. Apart from taxonomic classification, prey were also classified into functional categories based on their

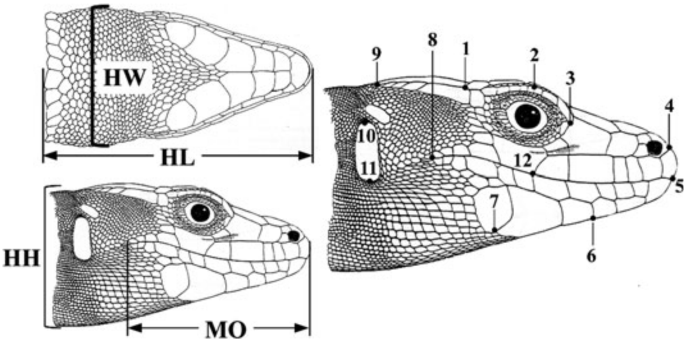

Fig. 1 Linear measurements taken in the head of the lizards and landmarks digitized for quantifying lateral head shape using geometric morphometrics. *HL* head length, *HW* head width, *HH* head height, *MO* mouth opening

hardness and mobility, which could potentially be more informative in ecological terms from the point of view of lizard foraging. Three hardness classes were distinguished based on previous hardness measurements obtained through prey-crushing (Herrel et al. 2001d; Verwaijen et al. 2002): adults of Araneae, Diptera, Hymenoptera, Lepidoptera, Mecoptera and Zygentoma, as well as all larvae, were considered as soft prey; adults of Dermaptera, Formicidae, Heteroptera and Homoptera were considered as intermediate-hardness prey; and adults of Coleoptera and Gastropoda were considered as hard prey. Based on their mobility (Perry and Pianka 1997), prey items were classified into sedentary (Dermaptera, Gastropoda and Heteroptera), walking/jumping (Araneae, Coleoptera, Formicidae, Homoptera, Zygentoma and all larvae) and flying categories (Diptera, Hymenoptera, Lepidoptera and Mecoptera).

Statistical analyses

To represent total head size (HS) we used Mosimann's (1970) geometric mean approach and calculated HS as the third root of the product of HL, HW and HH. We tested for intra- and interspecific differentiation in the quantified morphological traits using factorial univariate and multivariate analysis of variance ((M)ANOVA), with species (SP), sex (SEX), and their interaction (SP × SEX) as model effects. To gain more insight into potential allometric variation in morphological traits, we performed regression analyses between body size (SVL) and head size (HS), between all head dimensions and head size, and between lateral head shape and head size. We also included SP and SEX, as well as all the interaction terms, in the linear model, in order to test for differences in slopes and intercepts between groups.

To obtain a first idea of the morphological traits potentially relevant for bite force, we performed ANCOVA on bite force with SP and SEX as factors, and with each of the linear morphological traits (SVL, HS, head dimensions) treated separately as covariates. All interaction effects were also included. We then used model selection techniques (Burnham and Anderson 2002) to evaluate different models based on information theory (Akaike's Information Criterion) and to select the combination of linear body measurements that best explained variation in bite force. The relative importance of the different linear morphological variables was found as the sum of Akaike weights for that variable in all models with Delta AIC < 4 (Burnham and Anderson 2002). This procedure was performed on the pooled data, irrespective of species and sex, and in the four SP × SEX groups separately, to examine whether the importance of different morphological traits for determining bite force varied across groups. Finally, to assess how variation in lateral head shape was associated with variation in bite force across groups, we built a linear model of head shape on SP, SEX, bite force and all interaction effects. To visualize the interdependence between bite force and lateral head shape, we projected the shape data on the vector defined by the regression model to obtain individual regression scores that provide a graphical means to examine the strength of association between a multivariate response (shape) and a univariate predictor (bite force) (Drake and Klingenberg 2008; Adams and Nistri 2010).

Diet composition was characterized for each species-by-sex group by implementing the use index (UI). This index describes the importance of each prey type in the pellets examined by combining the percentage of pellets containing a given prey type with the percentage of its numeric abundance. The UI thus represents the homogeneity of consumption of a certain prey type throughout all pellets (see Carretero 2004 and references therein). We then compared use indices between sexes of the same species (sexual dietary disparity) and between species of the same sex (across-species disparity) using the graphical approach proposed by Carretero and Llorente (2001). We used Pianka's overlap index (Pianka 1973) to obtain a quantitative measure of similarity between groups (group disparity then being 1-overlap). As a complementary approach, we investigated whether the functional properties of prey (hardness and mobility) influenced their consumption by different SP × SEX groups using a Chi-squared test. We also tested whether SP × SEX groups differed in the size of consumed prey items, by concentrating on the most frequently used prey types, for which sufficient sample sizes were available. Here we calculated the total size of each prey item as the geometric mean of its length and width (both log-transformed) and then used a non-parametric ANOVA design based on 1,000 permutations to evaluate differences between SP × SEX groups in the size of consumed prey items. Finally, we performed two-way Mantel tests (Legendre and Legendre 1998) to test whether group differences in morphology (SVL, HS, head dimensions, lateral head shape) and bite force on one side and diet on the other where associated with each other. The Euclidean distance matrix was used for morphology and bite force, while the niche "distance" matrix (1—niche overlap) represented diet differentiation between groups.

All statistical analyses were conducted using R v. 2.12.1 (R Development Core Team 2010). Spline graphs representing differences between groups in geometric head shape were produced using Morpheus et al. software (Slice 1999), while deformation grids of variation across the bite-force variation range for different groups were produced using tpsRegr (Rohlf 2009).

Results

Morphological and performance differentiation

Analyses of morphology using (M)ANOVA indicated significant morphological differences between species and between the sexes, and in some cases significant interactions between factors (Table 1). Males of *P. bocagei* were significantly larger than conspecific females (Tukey HSD, $P = 0.02$), but no significant sexual dimorphism in total body size (e.g. logSVL) was observed in *P. hispanica* type 1A (Tukey HSD, $P = 0.67$) (Fig. 2a). Individuals of different species but of the same sex did not differ in total body size (Tukey HSD, $P > 0.05$ in both cases). A more prominent differentiation was observed across groups for HS, which differed significantly between all pairs except between females of the two species (Tukey HSD, $P = 0.16$). Males of both species had visibly larger heads than conspecific females, and males of *P. bocagei* had larger heads than those of *P. hispanica* type 1A (Table 1, Fig. 2b). Head dimensions all differed significantly between sexes, but not between species, with the exception of head height (HH). In all cases, male lizards had larger head dimensions than conspecific females. For head height (HH), all model terms were significant (Table 1) and post hoc comparisons showed that both species and sexes were significantly differentiated, where males had higher heads than females and individuals of *P. bocagei* had higher heads than those of *P. hispanica* type 1A (Fig. 2c).

Lateral head shape also differed between species and between the sexes (Table 1). Thin-plate spline deformation grids indicated that *P. hispanica* type 1A individuals of both sexes had relatively elongated but flattened lateral heads as compared to those of *P. bocagei* (Fig. 3a, b), while the males of both species displayed a relative expansion of the tympanic area (i.e. the area covered by landmarks 7–11, see Fig. 1), having relatively more robust heads as compared to females (Fig. 3c, d).

Table 1 Descriptive statistics and (M)ANOVA results for body size (SVL), linear head measurements, head size (HS), lateral head shape and bite force. All morphological traits are in mm and bite force readings in N (all at a logarithmic scale). Degrees of freedom are 3 (design) and 120 (residuals) in all comparisons. Values shown are the mean ± SE (top) and range (bottom). *F*-(top) and *P*-values (bottom) correspond to analysis of variance comparisons considering the effect of species (SP), sex and their interaction (SP × SEX). All *P*-values presented were corrected for multiple testing using the false discovery rate procedure. Significant effects are marked in bold letter

	PBF ($N = 29$)	PBM ($N = 32$)	PHF ($N = 30$)	PHM ($N = 33$)		SP	SEX	SP × SEX
logSVL	1.69 ± 0.01	1.72 ± 0.01	1.7 ± 0.01	1.71 ± 0.01	*F*	0.07	8.25	1.69
	1.59–1.78	1.63–1.78	1.62–1.77	1.61–1.78	*P*	0.79	**0.005**	0.20
logHS	0.9 ± 0.01	0.99 ± 0.01	0.88 ± 0.01	0.95 ± 0.01	*F*	15.98	133.24	0.83
	0.81–0.97	0.89–1.05	0.82–0.93	0.86–1.02	*P*	**<0.001**	**<0.001**	0.36
logHL	1.17 ± 0.01	1.25 ± 0.01	1.17 ± 0.01	1.24 ± 0.01	*F*	1.13	100.19	0.47
	1.06–1.24	1.15–1.32	1.1–1.23	1.15–1.34	*P*	0.29	**<0.001**	0.49
logHW	0.79 ± 0.01	0.89 ± 0.01	0.78 ± 0.01	0.87 ± 0.01	*F*	5.35	134.04	0.02
	0.7–0.89	0.78–0.99	0.71–0.83	0.74–0.94	*P*	**0.02**	**<0.001**	0.90
logHH	0.66 ± 0.01	0.75 ± 0.01	0.61 ± 0.01	0.68 ± 0.01	*F*	66.21	103.63	2.27
	0.56–0.75	0.67–0.83	0.54–0.69	0.58–0.75	*P*	**<0.001**	**<0.001**	0.13
logMO	0.97 ± 0.01	1.06 ± 0.01	0.95 ± 0.01	1.02 ± 0.01	*F*	10.55	125.30	1.23
	0.88–1.04	0.95–1.12	0.87–0.99	0.93–1.08	*P*	**0.002**	**<0.001**	0.27
GM shape[a]					*F*	15.57	12.28	0.89
					P	**<0.001**	**<0.001**	0.60
logBITE	0.11 ± 0.03	0.47 ± 0.03	0.02 ± 0.01	0.36 ± 0.03	*F*	10.63	155.34	0.00
	−0.17–0.37	0.00–0.70	−0.22–0.18	0.00–0.59	*P*	**0.002**	**<0.001**	0.98

[a] GM shape: lateral head shape as quantified using geometric morphometrics

Finally, bite force was significantly different between the sexes in both species ($P < 0.01$ for both species), but within each sex there were no differences between species ($P > 0.05$ in both sexes). In both species, males attained a higher maximal bite force than did females (Table 1, Fig. 2d).

Allometric patterns

Regression analyses between pairs of morphological traits indicated a significant association between body size and head size, head size and head dimensions, and head size and lateral head shape (Table 2). Comparison of regression coefficients among groups indicated significant differences in allometric trajectories between the sexes—but not between species—for the relationship between head size and body size, and between head size and lateral head shape (Table 2). Specifically, males of both species showed a more rapid increase of head size with increasing body size, and a steeper modification of lateral head shape with increasing head size (Fig. 4a, b). Additionally, there was a significant difference between species within the same sex in the regression intercept of head length and height with head size (Table 2), where both sexes of *P. bocagei* presented relatively shorter but higher heads than *P. hispanica* type 1A.

Considering form-function relationships, all biometric traits were shown to significantly influence bite force (Table 3). A difference in allometric trajectories between the sexes

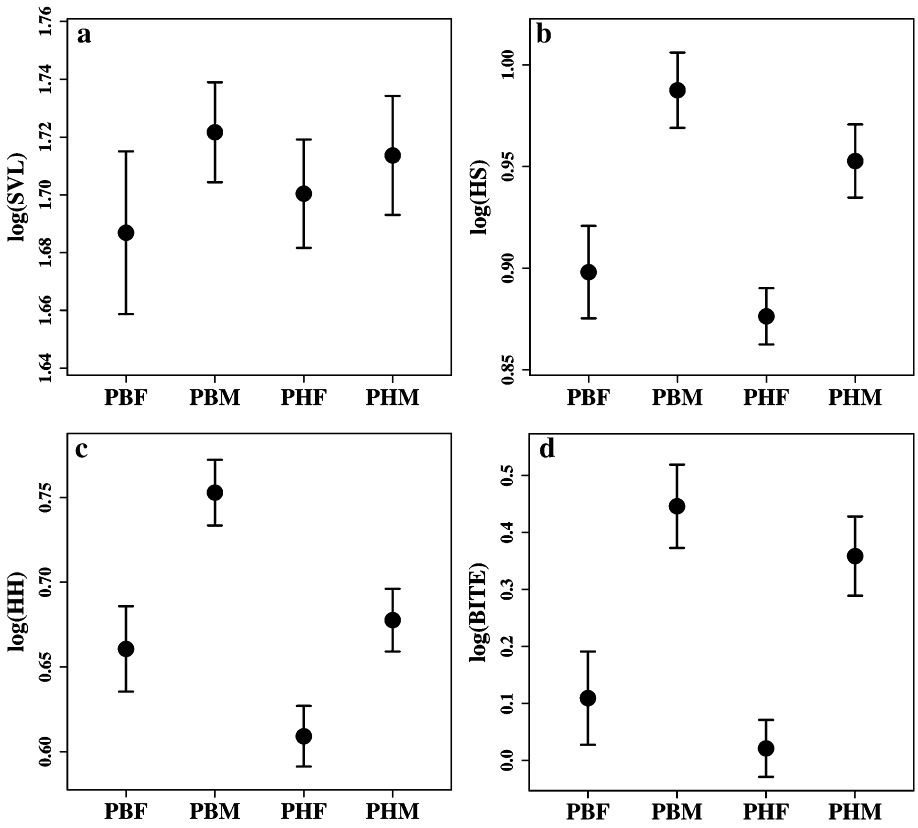

Fig. 2 Variation across groups in biometric traits (in mm) and bite force (in N). *Points* represent means and *vertical bars* denote 95% confidence intervals. *SVL* snout-vent length, *HS* head size, *HH* head height, *PBF P. bocagei* females, *PBM P. bocagei* males, *PHF P. hispanica* females, *PHM P. hispanica* males

existed for the relationship between bite force and body size (SVL), where males of both species presented slightly higher slopes than conspecific females (Table 3, Fig. 5a). The regression slope between bite force and head size was uniform across groups, but males were found to bite harder than females for the same head size, which was also the case for individuals of both sexes of *P. hispanica* type 1A as compared to those of *P. bocagei* (Table 3, Fig. 5b). Finally, a significant association was observed between lateral head shape and bite force, with a significant interaction between bite and sex (ANCOVA: $df = 7, 116$; P values for SP $= 3.51 \times 10^{-22}$, SEX $= 2.97 \times 10^{-21}$, bite $= 1.12 \times 10^{-5}$, SEX $\times$ bite $= 0.027$; all other effects $P > 0.1$). These results indicated that different structural relationships exist between lateral head shape and bite force in both sexes (but not species). In fact, in both species, a tight relationship exists between lateral head shape and bite force in males, whereas regression slopes are not significantly different from zero in females (Fig. 5c).

Model selection

Model selection indicated that the model that best described variation in bite force when examining all groups together included body size (SVL), head size (HS) and head width

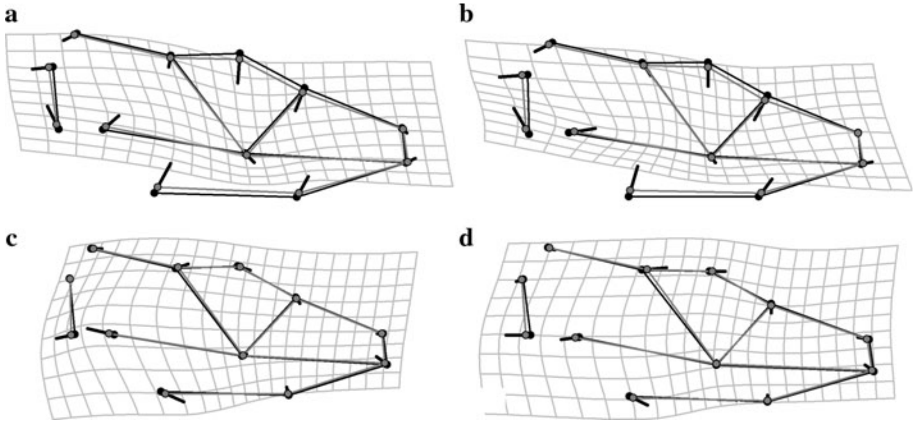

Fig. 3 Spline *graphs* depicting differences in lateral head shape as quantified through geometric morphometric methods between species and sexes. **a** Shape difference between species in males; **b**: shape difference between species in females; **c**: sexual dimorphism in *P. bocagei*; **d**: sexual dimorphism in *P. hispanica*. *Thick black lines* represent the vectors of change between the compared shapes and comparisons are always from *P. bocagei* to *P. hispanica* and from females to males. Shape patterns are exaggerated five-fold to enhance visualization

(HW) (Table 4). However, model selection results varied extensively across groups, with different variables being selected in different species and sexes. Globally, head size, head width and mouth opening were the most important variables across datasets (Table 4).

Dietary differentiation

Of the 124 lizards examined for morphology and bite force, we obtained pellets suitable for diet analyses from 100 individuals, containing a total of 440 prey items (prey per pellet ranging from one to twelve items). When dietary patterns were evaluated, indices of prey items revealed relatively low diet variation among groups, with the most frequently used prey types being Homoptera, Coleoptera, Diptera, Hymenoptera and Araneae. Graphical comparisons of food use indices revealed that the consumption of Homoptera and Coleoptera was slightly divergent between sexes in *P. bocagei* and between males of both species (Fig. 6a, c). By contrast, the sexes of *P. hispanica* type 1A, and females of both species, displayed almost identical food use patterns (Fig. 6b, d). Considering functional prey categories, neither prey hardness (Fig. 6e) nor prey mobility (Fig. 6f) showed an association with prey consumption by different groups (Hardness: $\chi^2 = 6.38$, $df = 6$, $P = 0.38$; Mobility: $\chi^2 = 8.21$, $df = 6$, $P = 0.22$). Comparison of prey size for the most commonly used prey items gave variable results: for Homoptera and Hymenoptera no significant differences were detected between the four lizard groups ($P > 0.05$ for all effects). By contrast, the size of consumed Coleoptera and Diptera differed between sexes (Coleoptera: $F = 4.501$, $P = 0.038$; Diptera: $F = 8.075$, $P = 0.011$), but not between species ($P > 0.05$ in both cases). Inspection of prey sizes revealed that significant effects of sex were due to *P. hispanica* type 1A females consuming smaller prey in both cases (Fig. 6g, h). Mantel tests associating food use with morphology and with bite force were not significant ($P > 0.1$ in all cases), except when Euclidean distances between group means for logSVL as the X matrix were used ($P = 0.033$).

Table 2 ANCOVA results for comparisons between species (SP) and sexes (SEX) on different combinations of biometric variables. *X*: effect of the covariate in the model (indicated in parenthesis next to the dependent variable); *F*: the *F* statistic, *P* the corresponding *P*-value after correction for multiple testing using the false discovery rate procedure. Degrees of freedom are 7 (design) and 116 (residuals) in all comparisons. Significant effects are marked in bold letter

	logHS (logSVL)		logHL (logHS)		logHW (logHS)		logHH (logHS)		logMO (logHS)		GM shape[a] (logHS)	
	F	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
X	1,321.52	**<0.001**	1,244.84	**<0.001**	2,516.02	**<0.001**	1,181.43	**<0.001**	3,826.84	**<0.001**	4.35	**<0.001**
SP	151.49	**<0.001**	37.11	**<0.001**	24.29	**<0.001**	94.6	**<0.001**	5.69	**0.03**	16.1	**<0.001**
SEX	606.87	**<0.001**	1.05	0.25	2.32	0.14	0.06	0.48	0.01	0.56	15.20	**<0.001**
X × SP	1.93	0.17	0.09	0.48	1.17	0.30	2.42	0.14	0.52	0.35	0.81	0.70
X × SEX	16.57	**<0.001**	0.58	0.35	3.67	0.08	1.41	0.21	2.28	0.14	1.72	**0.04**
SP × SEX	2.05	0.15	0.32	0.42	3.16	0.10	1.19	0.24	1.44	0.21	0.91	0.58
X × SP × SEX	0.15	0.48	0.06	0.48	0.00	0.56	0.13	0.48	0.09	0.48	0.70	0.82

[a] GM shape: lateral head shape as quantified using geometric morphometrics

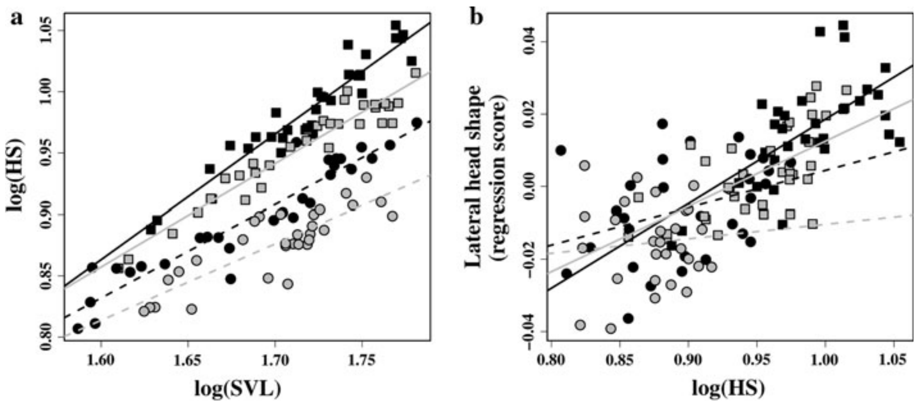

Fig. 4 Allometric relationship between head size and body size (**a**), lateral head shape as captured by geometric morphometrics and head size (**b**), head length and head size (**c**) and head height and head size (**d**). *Squares*, *continuous line*: males; *circles*, *dashed line*: females, *black*: *P. bocagei; grey*: *P. hispanica* type 1A. See Table 2 for tests of homogeneity of slopes and intercepts between groups

Discussion

Understanding the form-function relationship and its ecological implications is of central importance for understanding how morphological diversity evolves. Our study shows that the association between external morphology and performance traits can be quite flexible, such that different pressures can be reconciled for both ecological and social requirements to be met. In this system, external morphology is molded under the influence of both sexual and natural selection, but bite performance does not seem to be constrained due to morphological variation. The application of geometric morphometrics allows an integrated view of how different head components are modified to accommodate ecological pressures while maintaining performance, providing a powerful tool for future studies.

As commonly observed in *Podarcis* wall lizards (Braña 1996; Herrel et al. 1996; Kaliontzopoulou et al. 2007; Brecko et al. 2008; Kaliontzopoulou et al. 2008), both species examined here present marked sexual dimorphism in head size and shape. Males of both species have visibly larger heads than conspecific females (Fig. 2b), a pattern proximately caused by sexual differences in static allometry of head size on body size, where males present higher allometric slopes than females (Fig. 4a), as is common in many lacertid species (Braña 1996; Kratochvíl et al. 2003; Kaliontzopoulou et al. 2006, 2008). Geometric morphometrics also indicated sexual dimorphism in lateral head shape: males of both species present an inflation of the tympanic area as compared to conspecific females (Table 1; Fig. 3c, d). Interestingly, these patterns also coincide with what has been previously reported for *P. carbonelli* (Kaliontzopoulou et al. 2008), another member of the *P. hispanica* species complex (Kaliontzopoulou et al. 2011). Therefore, when our current findings are viewed in light of previous work, a maintenance of sexual shape patterns can be observed across this species complex, although only a phylogenetic comparative study including more members of this group could confirm this hypothesis. Furthermore, the relationship between head size and lateral head shape also shows important sexual allometric differentiation, where male head shape is markedly associated to head size, a pattern which is not observed in females (Fig. 4b). Put together, the above patterns provide

Table 3 Results obtained from linear models on bite force, with species (SP) and SEX as categorical predictors and different morphological predictors (BIOM) as covariates (specified in columns). *F* the *F*-statistic, *P*: the corresponding *P*-value after correction for multiple testing using the false discovery rate procedure. Degrees of freedom are 7 (design) and 116 (residuals) in all comparisons. Significant effects are marked in bold letter

	logSVL		logHS		logHL		logHW		logHH		logMO	
	F	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
BIOM	432.17	**<0.001**	1066.82	**<0.001**	560.77	**<0.001**	999.73	**<0.001**	538.86	**<0.001**	872.13	**<0.001**
SP	36.69	**<0.001**	1.68	0.13	12.33	**<0.001**	3.90	**0.04**	43.41	**<0.001**	0.03	0.38
SEX	306.59	**<0.001**	12.09	**<0.001**	31.02	**<0.001**	11.32	**<0.001**	31.83	**<0.001**	17.77	**<0.001**
BIOM × SP	1.57	0.13	0.15	0.34	1.01	0.18	1.15	0.17	0.09	0.36	0.01	0.39
BIOM × SEX	6.91	**0.01**	0.16	0.34	0.06	0.37	0.87	0.19	0.10	0.36	2.05	0.11
SP × SEX	5.86	**0.02**	5.40	**0.02**	4.34	**0.03**	1.68	0.13	8.45	**<0.001**	10.92	**<0.001**
BIOM × SP × SEX	0.02	0.38	1.21	0.17	0.74	0.20	0.76	0.2	5.16	**0.02**	1.84	0.13

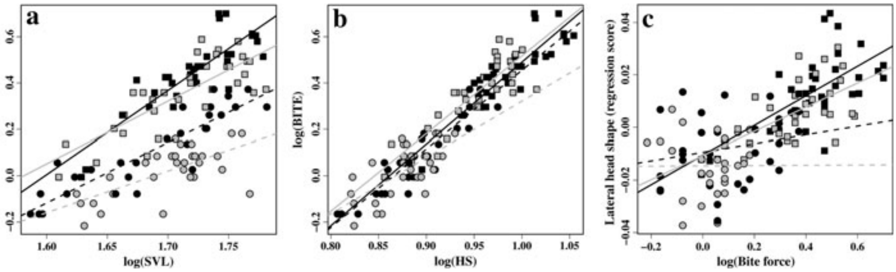

Fig. 5 Allometric relationship between morphological traits and bite force. *Squares*, *continuous line*: males; *circles*, *dashed line*: females; *black*: *P. bocagei*; *grey*: *P. hispanica* type 1A. See Table 3 for tests of homogeneity of slopes and intercepts between groups

Table 4 Model selection statistics on different models of bite force including linear combinations of morphological measurements for the complete dataset (all) and for each group separately (*PBF P. bocagei* females, *PBM P. bocagei* males, *PHF P. hispanica* females, *PHM P. hispanica* males). Regression coefficients for the best model (BM) based on Akaike's Information Criterion are presented below each predictor. *R^2* adjusted R^2, *AICc*: Akaike's Information Criterion corrected for small samples. *VI*: variable importance as the sum of Akaike weights for each variable across the set of models with deltaAICc < 4 (Burnham and Anderson 2002). The two most important variables for each dataset are indicated in bold letter

		Intercept	logSVL	logHS	logHL	logHW	logHH	logMO	R^2	AICc
All	BM	−2.31	−0.51	2.29		1.56			0.9	−290.99
	VI		0.91	**0.92**	0.14	**1**	0.21	0.23		
PBF	BM	−2.94		3.39					0.88	−77.32
	VI		0.09	**0.81**	0.27	0.33	0.20	**0.34**		
PBM	BM	−2.92				1.56		1.88	0.83	−76.58
	VI		0.13	0.29	0.16	**0.83**	0.16	**0.68**		
PHF	BM	−1.87				2.44			0.53	−67.42
	VI		0.19	0.14	0.14	**1**	0.08	**0.30**		
PHM	BM	−2.63		2.24			1.26		0.76	−70.58
	VI		0.22	**0.63**	0.37	0.23	**0.65**	0.27		

indirect morphological evidence to the action of sexual selection on head relative size and shape (Andersson 1994; Bonduriansky and Day 2003; Bonduriansky 2007).

Focusing on interspecific patterns, head size also differs between species, with *P. bocagei* having bigger heads than *P. hispanica* type 1A, although this pattern is only significant for males (Fig. 2b). Both species are also significantly differentiated in head shape, as indicated by both linear and geometric morphometrics (Table 1, 2). Both patterns of lateral head shape (deformation grids, Fig. 3a, b) and ANCOVA on linear head dimensions with head size as a covariate (Fig. 4c, d) indicate that, in both sexes, *P. bocagei* has a relatively shorter and higher head, with a more robust built, as compared to *P. hispanica* type 1A. The morphological differentiation observed between *P. bocagei* and *P. hispanica* type 1A has been related to the marked microhabitat divergence between both species (Sá-Sousa 2001). The smaller and flatter head of *P. hispanica* type 1A likely reflects this species' preference for inhabiting saxicolous habitats, in contrast to the more ground-dwelling habits of *P. bocagei* (Sá-Sousa et al. 2002), a pattern typical of rock-dwelling lacertids (Arnold 1973, 1987). Interestingly, both linear head dimensions and

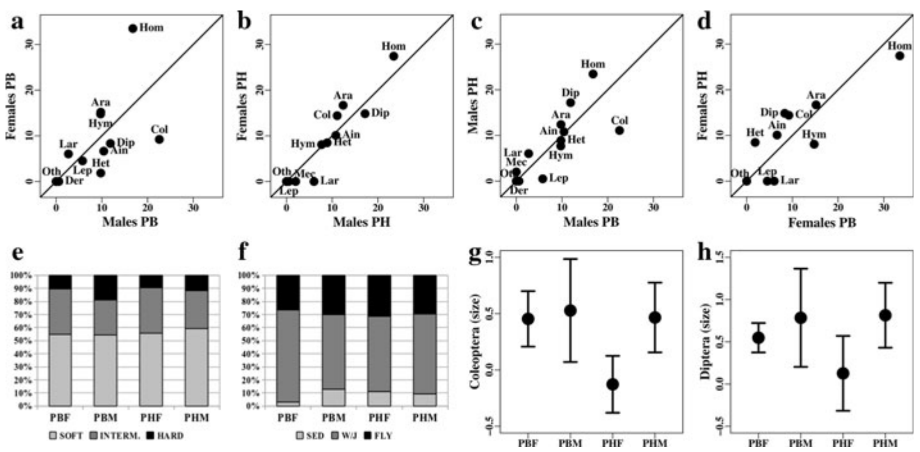

Fig. 6 Dietary patterns observed across the four examined groups. **a**–**d** Scatter-plots comparing group use indices for each of the prey types consumed between both sexes in *P. bocagei* (**a**) and *P. hispanica* type 1A (**b**), as well as between species in males (**c**) and females (**d**). The *continuous line* represents a slope of 1, i.e. equal use of food resources for the compared groups. *Ain* Indeterminate arthropods, *Ara* Araneida, *Col* Coleoptera, *Der* Dermaptera, *Dip* Diptera, *Het* Heteroptera, *Hom* Homoptera, *Hym* Hymenoptera, *Lar* Larvae, *Lep* Lepidoptera, *Mec* Mecoptera. *PBF P. bocagei* females, *PBM P. bocagei* males, *PHF P. hispanica* type 1A females, *PHM P. hispanica* males type 1A. **e**–**f**: Percentage of functional prey types consumed by each group according to prey hardness (**e**) and mobility (**f**). *SED* sedentary, *W/J* walking/jumping, *FLY* flying. **g**–**h** Prey size patterns for prey types in which significant differences between groups were detected (**e**: Coleoptera, **f**: Diptera; see "Results")

lateral head shape show similar patterns of static allometry with head size in both species, a fact that may be indicative of a preserved head size-shape relationship across species, but once again only a comparison including more species can confirm this hypothesis. Intriguingly, different studies of head shape-size allometry in lacertids have given different results. While relative uniformity is observed across species in some cases (Kaliontzopoulou et al. 2008; present study), extensive variation has been reported in others (Ljubisavljević et al. 2010) and ontogenetic variation has been recently suggested to be a major source of shape variability in *Podarcis* lizards (Piras et al. 2011), pointing to a potentially very fruitful field for future investigation.

But how are the above intersexual and interspecific morphological patterns associated with bite performance? Our results show that making predictions about performance based on morphological information alone is not straight-forward; for while significant functional sexual dimorphism exists in both species examined, bite force does not differ between species when considering individuals of the same sex (Table 1). Despite their smaller and visibly flatter heads, males of *P. hispanica* type 1A bite equally hard as those of *P. bocagei* (Fig. 2d). Thus, although microhabitat divergence between species is reflected in their general head shape, this does not constrain bite performance. Future studies using phylogenetic comparative methods to investigate morphological and performance variation in this group of lizards would shed more light into how natural selection associated to microhabitat use may contribute in shaping phenotypic divergence. Importantly, morphological patterns support the hypothesis that an interaction between sexual and natural selection may occur in this system. Considering variation in head height, a head dimension that is frequently mechanically constrained in saxicolous lizards (Arnold 1973, 1987, 1998), we observe a significant interaction term (Table 1), indicating that sexual dimorphism varies across species, *P. bocagei* being more dimorphic than *P. hispanica* type 1A (Fig. 2c). A potential explanation for this pattern is that natural selection associated to microhabitat use and predator escape is limiting the optimal increase of head height in *P. hispanica* type 1A males under the effect of sexual selection, as has been observed in other lizards (Vitt et al. 1997; Stuart-Fox and Moussalli 2007). However, our results indicate that both ecological and social demands can be fulfilled in this system, by modification of morphology-performance relationships across species.

Model evaluation procedures indicate that head size, head width and mouth opening are the main determinants of bite performance in our system (Table 4). Head size and width have been previously shown to be good predictors of bite force and in many cases explains variation in bite performance among individuals (Herrel et al. 2001a; Lappin et al. 2006; Huyghe et al. 2009). However, model evaluation procedures also show that the morphological variables most correlated with bite performance vary extensively across species and sexes, thus indicating that this is a highly flexible and dynamic system. In this context, our study indicates that the variation observed across different lizard taxa concerning the external morphological variables that most highly correlate with bite force and are thus considered good performance predictors may be due to variation in ecological and social characteristics across these groups. We must also point out that, at the proximate level, functional similarity can also be achieved by modification of the jaw muscle insertion points, and/or the orientation and length of muscles (Herrel et al. 1996, 1998a, 2001a). Thus, a detailed study of bite biomechanics and anatomy of the jaw musculature in these lizards would enable one to tease apart how different morphological traits and structures might compensate among them to produce similar performance functionality (Alfaro et al. 2004; Toro et al. 2004; Alfaro et al. 2005).

Nevertheless, a more detailed and complete image of how head shape varies across species and sexes is provided by the use of geometric morphometric methods, which allow a better understanding of how the flatter head of *P. hispanica* type 1A may be compensated for in terms of bite force. Indeed, deformation grids show that although individuals of both sexes of *P. hispanica* type 1A are relatively flatter than those of *P. bocagei*, they also present an amplification of the tympanic area (Fig. 3a, b). This is achieved through the posterior displacement of the ear opening (landmarks 10 and 11, see Fig. 1) and by the anterior displacement of the posterior limit of the mouth (landmark 8). As is true for sexual dimorphism patterns (see above), such a shape modification provides more space for the jaw adductor muscle, potentially enhancing bite force in *P. hispanica* type 1A. This example nicely illustrates how geometric morphometric techniques can improve the study of biomechanical systems. Were only linear biometric traits included in this study, this kind of shape modification, relevant for understanding the observed patterns of functional variation, would have been missed (see also Adams and Rohlf 2000). Further, we also find a direct association between geometric lateral head shape and bite force, significant only in males and with a common slope between species (Fig. 5c). In this context, head shape and bite force seem to be integrated through the influence of head size, which scales allometrically between sexes with head shape (Fig. 5c). Thus, allometric head shape modification in males likely increases the performance advantages obtained through a relatively bigger head, further augmenting bite force. This observation is also consistent with biomechanical predictions, since an amplification of the tympanic area provides more space for a more developed set of jaw adductor muscles (Herrel et al. 1996), and lends further support to the importance of sexual selection in shaping morphological patterns by enhancing bite force in males.

Based on the observed morphological and performance differentiation, we may also expect a dietary divergence, particularly between sexes, in respect to the type and size of prey consumed. In fact, head size and shape variation have been frequently associated with dietary divergence (Adams and Rohlf 2000; Herrel et al. 1996, 2001d; Verwaijen et al. 2002; Maerz et al. 2006; Vincent and Herrel 2007; Brecko et al. 2008). Nonetheless, our analysis of dietary divergence provided little support for this prediction, contradicting previous observations in other lacertid species (i.e. Vincent and Herrel 2007 and references therein). For instance, prey consumption did not vary much across the four SP × SEX groups examined, although some localized differences did exist. Specifically, male *P. bocagei* consumed relatively less Homoptera and more Coleoptera than conspecific females or male *P. hispanica* type 1A (Fig. 6a, c), while female *P. hispanica* type 1A consumed significantly smaller Coleoptera and Diptera than the remaining groups (Fig. 6g, h). These results indicate a tendency towards differential prey consumption by some groups, the detection of which might be restricted by low statistical power due to low sample sizes in terms of retrieved prey items per pellet, or the examination of a single sampling event, not taking seasonal variation in diet into account. Previous studies have drawn the attention to the fact that in most cases field dietary data do not offer sufficient resolution to assess ecological divergence (Herrel et al. 2001b). In fact, our results rather indicate a significant association between dietary divergence and differences between groups in total body size, possibly pointing to the influence of other factors, such as foraging tactics (McBrayer 2004; Schwenk 2000), predation pressure and time-energy budgets during prey consumption, or even microhabitat use (Arnold 1987), which may be relatively more influential on prey utilization (e.g. Diaz 1995; Herrel et al. 2001d; Carretero 2004).

Together, our findings indicate that although body and head size are tightly linked to bite performance in these two *Podarcis* species, in accordance with previous studies, they are rather secondary in explaining the observed functional variation. Instead, head dimensions and head shape also play an important role in determining bite performance, thereby providing the potential for the maintenance of equivalent performance under different head configurations. In fact, this system provides a nice example of relatively rapid morphological differentiation (*P. bocagei* and *P. hispanica* type 1 diverged approximately 5.5 MYA, i.e. Kaliontzopoulou et al. 2011), without concordant functional divergence between two sister groups of lizards. Furthermore, our results indicate that group differentiation in head size and shape and bite force is not reflected in the dietary similarity neither between species nor between sexes, suggesting that the evolutionary causation of the observed morphological and performance patterns should be sought elsewhere. Given the close relationship between head morphology and bite performance observed across sexes, we conclude that the form-function association in lizards is tightly linked to the observed sexual dimorphism in both aspects, with sexual selection potentially being the underlying evolutionary force, as has been proven for other lizard groups (Husak et al. 2006a; Lailvaux and Irschick 2006). However, such a hypothesis can only be definitely confirmed by directly examining the reproductive fitness of male individuals and associating it to both head morphology and bite performance (Lappin and Husak 2005; Irschick et al. 2007), as has been done for the form-locomotor performance complex (Husak et al. 2006b; Husak and Fox 2008).

Acknowledgments We thank Catarina Rato and Fatima Jorge for help during fieldwork and experimental treatments. Anthony Herrel kindly provided the force transducer used for bite-force measurements. Two anonymous reviewers provided insightful comments that aided in improving a previous version of the manuscript. AK, AvdM and AP were supported by post-doctoral grants (SFRH/BPD/68493/2010, SFRH/BPD/48042/2008 and SFRH/BPD/26546/2006 respectively), all from Fundação para a Ciência e Tecnologia (FCT, Portugal), and DCA was supported in part by NSF grant DEB-0446758. Capture and handling of the animals used were performed under a scientific permit provided by Instituto para a Conservação da Natureza e Biodiversidade (ICNB, Portugal).

References

Adams DC (2004) Character displacement via aggressive interference in *Appalachian salamanders*. Ecology 85:2664–2670

Adams DC, Nistri A (2010) Ontogenetic convergence and evolution of foot morphology in European cave salamanders (Family: Plethodontidae). BMC Evol Biol 10(216):1–10

Adams DC, Rohlf FJ (2000) Ecological character displacement in *Plethodon*: biomechanical differences found from a geometric morphometric study. Proc Nat Acad Sci USA 97:4106–4111

Adams DC, Rohlf FJ, Slice DE (2004) Geometric morphometrics: ten years of progress following the 'revolution'. Ital J Zool 71:5–16

Alfaro ME, Bolnick DI, Wainwright PC (2004) Evolutionary dynamics of complex biomechanical systems: an example using the four-bar mechanism. Evolution 58:495–503

Alfaro ME, Bolnick DI, Wainwright PC (2005) Evolutionary consequences of many-to-one mapping of jaw morphology to mechanics in labrid fishes. Am Nat 165:E140–E154

Andersson M (1994) Sexual selection: monographs in behavior and ecology. Princeton University Press, Princeton

Arnold EN (1973) Relationships of the Palearctic lizards assigned to the genera *Lacerta*, *Algyroides* and *Psammodromus* (Reptilia: Lacertidae). Bull Br Mus 25:289–366

Arnold SJ (1983) Morphology, performance and fitness. Am Zool 23:347–361

Arnold EN (1987) Resource partition among lacertid lizards in southern Europe. J Zool Lond (B) 1:739–782

Arnold EN (1998) Cranial kinesis in lizards: variations, uses and origins. Evol Biol 30:323–357

Bonduriansky R (2007) Sexual selection and allometry: a critical reappraisal of the evidence and ideas. Evolution 61:838–849

Bonduriansky R, Day T (2003) The evolution of static allometry in sexually selected traits. Evolution 57:2450–2458

Bookstein FL (1991) Morphometric tools for landmark data: geometry and biology. Cambridge University Press, Cambridge

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

Brecko J, Huyghe K, Vanhooydonck B, Herrel A, Grbac I (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

Bruner E, Constantini D (2007) Head morphological variation in *Podarcis muralis* and *Podarcis sicula*: a landmark-based approach. Amphib Reptilia 28:566–573

Burnham KP, Anderson DR (2002) Model selection and multi-model inference: a practical-theoretic approach, 2nd edn. Springer, New York

Butler MA, Losos JB (2002) Multivariate sexual dimorphism, sexual selection, and adaptation in Greater Antillean *Anolis* lizards. Ecol Monogr 72:541–559

Butler MA, Sawyer SA, Losos JB (2007) Sexual dimorphism and adaptive radiation in *Anolis* lizards. Nature 447:202–205

Carretero MA (2004) Form set menu to *a la carte*. Linking issues in trophic ecology of Mediterranean lizards. Ital J Zool Supp 2:121–133

Carretero MA (2008) An integrated assessment of the specific status in a group with complex systematics: the Iberomaghrebian lizard genus *Podarcis* (Squamata, Lacertidae). Integr Zool 4:247–266

Carretero MA, Llorente GA (2001) What are they really eating? Stomach *versus* intestine as sources of diet information in lacertids. In: Vicente L, Crespo EG (eds) Mediterranean basin lacertid lizards: a biological approach. ICN, Lisbon, pp 105–112

Cooper WE Jr., Vitt LJ (1989) Sexual dimorphism of head and body size in an iguanid lizard: paradoxical results. Am Nat 133:729–735

Diaz JA (1995) Prey selection by lacertid lizards: a short review. Herp J 5:245–251

Drake AG, Klingenberg CP (2008) The pace of morphological change: historical transformation of skull shape in St Bernard dogs. Proc R Soc B 275:71–76

Harris DJ, Sá-Sousa P (2002) Molecular phylogenetics of Iberian Wall Lizards (*Podarcis*): is *Podarcis hispanica* a species complex? Mol Phylogenet Evol 23:75–81

Herrel A, O'Reilly JC (2006) Ontogenetic scaling of bite force in lizards and turtles. Phys Biochem Zool 79:31–42

Herrel A, Van Damme R, de Vree F (1996) Sexual dimorphism of head size in *Podarcis hispanica atrata*: testing the dietary divergence hypothesis by bite force analysis. Neth J Zool 46:253–262

Herrel A, Aerts P, De Vree F (1998a) Ecomorphology of the lizard feeding apparatus: a modelling approach. Neth J Zool 48:1–25

Herrel A, Aerts P, De Vree F (1998b) Static biting in lizards: functional morphology of the temporal ligaments. J Zool Lond 244:135–143

Herrel A, de Grauw E, Lemos-Espinal JA (2001a) Head shape and bite performance in xenosaurid lizards. J Exp Zool 290:101–107

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

Herrel A, Meyers J, Nishikawa KC, De Vree F (2001c) The evolution of feeding motor patterns in lizards: modulatory complexity and possible constraints. Am Zool 41:1311–1320

Herrel A, Van Damme R, Vanhooydonck B, De Vree F (2001d) The implications of bite performance for diet in two species of lacertid lizards. Can J Zool 79:662–670

Herrel A, McBrayer LD, Larson PM (2010) Functional basis for sexual differences in bite force in the lizard *Anolis carolinensis*. Biol J Linn Soc 91:111–119

Husak JF, Fox SF (2008) Sexual selection on locomotor performance. Evol Ecol Res 10:213–228

Husak JF, Lappin AK, Fox SF, Lemos-Espinal JA (2006a) Bite-force performance predicts dominance in male venerable collared lizards (*Crotaphytus antiquus*). Copeia 2006:301–306

Husak JF, Fox SF, Lovern MB, van den Bussche RA (2006b) Faster lizards sire more offspring: sexual selection on whole-animal performance. Evolution 60:2122–2130

Husak JF, Lappin AK, van den Bussche RA (2009) The fitness advantage of a high-performance weapon. Biol J Linn Soc 96:840–845

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

Huyghe K, Herrel A, Adriaens D, Tadić Z, Van Damme R (2009) It is all in the head: morphological basis for differences in bite force among colour morphs of the Dalmatian wall lizard. Biol J Linn Soc 96:13–22

Irschick DJ, Herrel A, Vanhooydonck B, Van Damme R (2007) A functional approach to sexual selection. Funct Ecol 21:621–626

Irschick DJ, Meyers JJ, Husak JF, Le Galliard JF (2008) How does selection operate on whole-organism functional performance capacities? A review and synthesis. Evol Ecol Res 10:177–196

Kaliontzopoulou A, Carretero MA, Llorente GA (2006) Patterns of shape and size sexual dimorphism in a population of *Podarcis hispanica** (Reptilia: Lacertidae) from NE Iberia. In: Corti C, Lo Cascio P, Biaggini M (eds) Mainland and insular lacertid lizards: a mediterranean perspective. Firenze University Press, Firenze, pp 73–89

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

Kaliontzopoulou A, Carretero MA, Llorente GA (2008) Head shape allometry and proximate causes of head sexual dimorphism in *Podarcis* lizards: joining linear and geometric morphometrics. Biol J Linn Soc 93:111–124

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

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

Kingsolver J, Huey RB (2003) Introduction: the evolution of morphology, performance, and fitness. Integr Comp Biol 43:361–366

Kratochvíl L, Frynta D (2002) Body size, male combat and the evolution of sexual dimorphism in eublepharid geckos (Squamata: Eublepharidae). Biol J Linn Soc 76:303–314

Kratochvíl L, Fokt M, Rehák I, Frynta D (2003) Misinterpretation of character scaling: a tale of sexual dimorphism in body shape of common lizards. Can J Zool 81:1112–1117

Lailvaux SP, Irschick DJ (2006) A functional perspective on sexual selection: insights and future prospects. Anim Behav 72:263–273

Lailvaux SP, Irschick DJ (2007) The evolution of performance-based male fighting ability in Caribbean *Anolis* lizards. Am Nat 170:573–586

Lappin AK, Husak JF (2005) Weapon performance, not size, determines mating success and potential reproductive output in the collared lizard (*Crotaphytus collaris*). Am Nat 166:426–436

Lappin AK, Hamilton PS, Sullivan BK (2006) Bite-performance and head shape in a sexually dimorphic crevice-dwelling lizard, the common chuckwalla [*Sauromalus ater* (=*obesus*)]. Biol J Linn Soc 88:215–222

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

Ljubisavljević K, Urosević A, Aleksić I, Ivanović A (2010) Sexual dimorphism of skull shape in a lacertid lizard species (*Podarcis* spp., *Dalmatolacerta* sp., *Dinarolacerta* sp.) revealed by geometric morphometrics. Zoology 113:168–174

Losos JB, Butler MA, Schoener TW (2003) Sexual dimorphism in body size and shape in relation to habitat use among species of Caribbean *Anolis* lizards. In: Fox SF, McCoy JK, Baird TA (eds) Lizard social behaviour. John Hopkins University Press, Baltimore, pp 356–380

Maerz JC, Myers EM, Adams DC (2006) Trophic polymorphism in a terrestrial salamander. Evol Ecol Res 8:23–35

McBrayer LD (2004) The relationship between skull morphology, biting performance and foraging mode in Kalahari lacertid lizards. Zool J Linn Soc 140:403–416

Measey GJ, Hopkins K, Tolley KA (2009) Morphology, ornaments and performance in two chameleon ecomorphs: is the casque bigger than the bite? Zoology 112:217–226

Metzger KA, Herrel A (2005) Correlations between lizard cranial shape and diet: a quantitative, phylogenetically informed analysis. Biol J Linn Soc 86:433–466

Mosimann JE (1970) Size allometry: size and shape variables with characterizations of the lognormal and generalized gamma distributions. J Am Stat Assoc 65:930–945

Perrin N, Travis J (1992) On the use of constraints in evolutionary biology and some allergic reactions to them. Funct Ecol 6:361–363

Perry G, Pianka ER (1997) Animal foraging: past, present and future. Trends Ecol Evol 12:360–364

Pianka ER (1973) The structure of lizard communities. Annu Rev Ecol Syst 4:53–74

Pinho C, Ferrand N, Harris DJ (2006) Reexamination of the Iberian and North African *Podarcis* (Squamata: Lacertidae) phylogeny based on increased mitochondrial DNA sequencing. Mol Phylogenet Evol 38:266–273

Piras P, Salvi D, Ferrara G, Maiorino L, Delfino M, Pedde L, Kotsakis T (2011) The role of postnatal ontogeny in the evolution of phenotypic diversity in *Podarcis* lizards. J Evol Biol (in press)

Preest MR (1994) Sexual size dimorphism and feeding energetics in *Anolis carolinensis*: why do females take smaller prey than males? J Herpetol 28:292–298

Raia P, Guarino FM, Turano M, Polese G, Rippa D, Carotenuto F, Monti DM, Cardi M, Fulgione D (2010) The blue lizard spandrel and the island syndrome. BMC Evol Biol 10:289

Rivera G (2008) Ecomorphological variation in shell shape of the freshwater turtle *Pseudemys concinna* inhabiting different aquatic flow regimes. Integr Comp Biol 48:769–787

Rohlf FJ (2005) tpsDig, digitize landmarks and outlines, version 2.04. Department of Ecology and Evolution, State University of New York at Stony Brook, Stony Brook

Rohlf FJ (2008) tpsRelw, relative warps analysis, version 1.46. Department of Ecology and Evolution, State University of New York at Stony Brook, Stony Brook

Rohlf FJ (2009) tpsRegr, version 1.37. Department of Ecology and Evolution, State University of New York at Stony Brook, Stony Brook

Rohlf FJ, Marcus LF (1993) A revolution in morphometrics. Trends Ecol Evol 8:129–132

Rohlf FJ, Slice DE (1990) Extensions of the Procrustes method for the optimal superimposition of landmarks. Syst Zool 39:40–59

Sá-Sousa P (2001) A controversa sistemática das lagartixas do género *Podarcis* Wagler, 1830 (Sauria, Lacertidae) em Portugal. PhD thesis, University of Lisbon, Lisbon

Sá-Sousa P, Vicente L, Crespo EG (2002) Morphological variability of *Podarcis hispanica* (Sauria: Lacertidae) in Portugal. Amphib Reptilia 23:55–69

Schwenk K (2000) Feeding in lepidosaurs. In: Schwenk K (ed) Feeding: form, function and evolution in tetrapod vertebrates. Academic Press, San Diego, pp 175–291

Slice DE (1999) Morpheus et al.: software for morphometric research. Department of Ecology and Evolution, State University of New York, Stony Brook

Slice DE (2005) Modern morphometrics. In: Slice DE (ed) Modern morphometrics in physical anthropology. Kluwer, New York, pp 1–46

Stamps J (1983) Sexual selection, sexual dimorphism and territoriality. In: Huey RB, Pianka ER, Schoener TW (eds) Lizard ecology: studies of a model organism. Harvard University Press, Cambridge, pp 169–204

Stuart-Fox D, Moussalli A (2007) Sex-specific ecomorphological variation and the evolution of sexual dimorphism in dwarf chameleons (*Bradypodion* spp.). J Evol Biol 20:1073–1081

R Development Core Team (2010) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. http://www.R-project.org

Toro E, Herrel A, Irschich D (2004) The evolution of jumping performance in Caribbean *Anolis* lizards: solutions to biomechanical trade-offs. Am Nat 163:844–856

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

Verwaijen D, Van Damme R, Herrel A (2002) Relationships between head size, bite force, prey handling efficiency and diet in two sympatric lacertid species. Funct Ecol 16:842–850

Vincent SE, Herrel A (2007) Functional and ecological correlates of ecologically-based dimorphisms in squamate reptiles. Integr Comp Biol 47:172–188

Vitt LJ, Caldwell JP, Zani PA, Titus TA (1997) The role of habitat shift in the evolution of lizard morphology: evidence from tropical *Tropidurus*. Proc Nat Acad Sci USA 94:3828–3832

Wainwright PC (2007) Functional versus morphological diversity in macroevolution. Annu Rev Ecol Evol Syst 38:381–401

Walker JA (2007) A general model of functional constraints on phenotypic evolution. Am Nat 170:681–689

Young MT, Brusatte SL, Ruta M, De Andrade MB (2010) The evolution of Metriorhynchoidea (Mesoeucrocodylia, Thalattosuchia): an integrated approach using geometric morphometrics, analysis of disparity, and biomechanics. Zool J Linn Soc 158:801–859