

# Ecomorphological variation in male and female wall lizards and the macroevolution of sexual dimorphism in relation to habitat use

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## Abstract

Understanding how phenotypic diversity evolves is a major interest of evolutionary biology. Habitat use is an important factor in the evolution of phenotypic diversity of many animal species. Interestingly, male and female phenotypes have been frequently shown to respond differently to environmental variation. At the macroevolutionary level, this difference between the sexes is frequently analysed using phylogenetic comparative tools to assess variation in sexual dimorphism (SD) across taxa in relation to habitat. A shortcoming of such analyses is that they evaluate the degree of dimorphism itself and therefore they do not provide access to the evolutionary trajectories of each sex. As such, the relative contribution of male and female phenotypes on macroevolutionary patterns of sexual dimorphism cannot be directly assessed. Here, we investigate how habitat use shapes phenotypic diversity in wall lizards using phylogenetic comparative tools to simultaneously assess the tempo and mode of evolution in males, females and the degree of sexual dimorphism. We find that both sexes have globally diversified under similar, but not identical, processes, where habitat use seems to drive macroevolutionary variation in head shape, but not in body size or relative limb length. However, we also observe small differences in the evolutionary dynamics of male and female phenotypes that have a marked impact on macroevolutionary patterns of SD, with important implications for our interpretation of what drives phenotypic diversification within and between the sexes.

## Introduction

Understanding how environmental variation drives phenotypic diversification is a major objective in evolutionary biology. The animal kingdom thrives with examples of morphological traits that are recurrently linked to life in a specific environment. Morphological variation in relation to structural niche represents one of the most striking patterns of phenotype–environment

matching, and habitat use has been frequently pinpointed as an important factor driving the evolution of phenotypic diversity in many animal species. This association represents a classic case of the ecomorphological paradigm (Arnold, 1983), where an association between ecological and morphological variation is established through evolutionary influences on functional traits. Here, selection operates on whole-organism performance so as to maximize the ability of individuals for fulfilling their ecological tasks. This evolutionary influence then translates into morphological variation across habitats through biomechanical links between morphology and performance (Irschick *et al.*, 2008).

Interestingly, ecomorphological variation is not always uniform in both sexes. This is because, in many

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cases, the functional and morphological traits used for fulfilling ecological tasks are also relevant for social functions, meaning that both natural and sexual selection are frequently involved in determining how they vary across different environments (Cox *et al.*, 2007). Indeed, the different reproductive roles adopted by males and females in anisogamous organisms yield differences in the selective regimes experienced by individuals of each sex (Fairbairn, 1997; Blanckenhorn, 2000). A review of available data indicates that natural and sexual selection operate in the same direction, at least at the intraspecific level (Irschick *et al.*, 2008). However, several studies also suggest that complex evolutionary interactions may take place, as males and females have been frequently reported to respond differently to environmental factors, causing variation in the degree of SD across different habitats, both at the intraspecific (Stuart-Fox & Moussalli, 2007; Kaliontzopoulou *et al.*, 2010a) and macroevolutionary levels (Butler *et al.*, 2000; Butler & Losos, 2002). As such, comparisons of SD across populations of a single species, or macroevolutionary comparisons among species, seek to understand how differences in ecological or other traits modify this balance across populations or taxa (Fairbairn *et al.*, 2007).

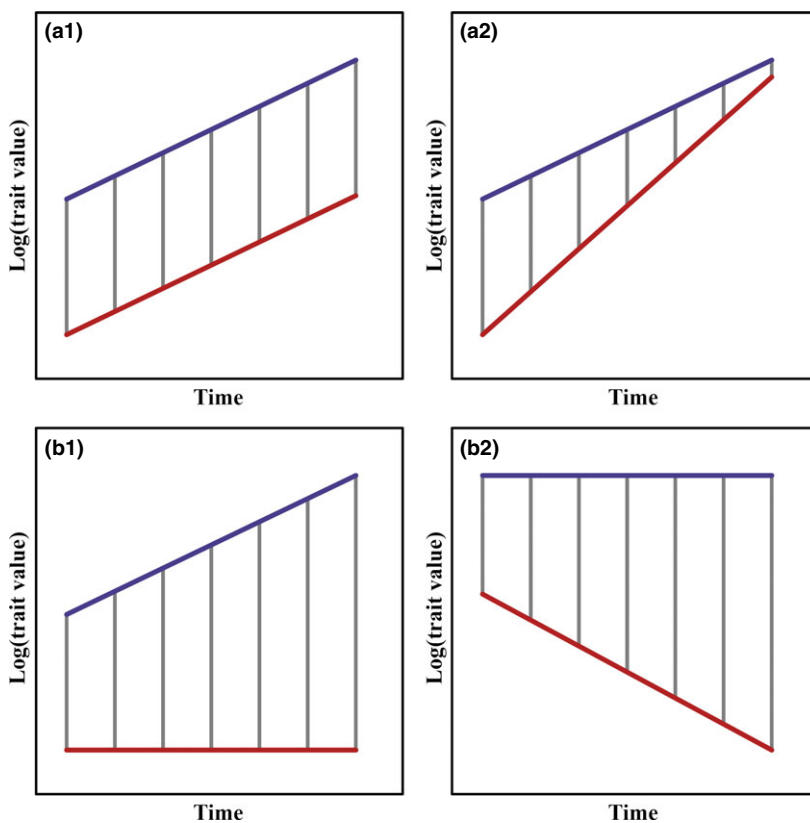
There are, however, substantial procedural differences when examining variation in SD in relation to habitat use within species *versus* when investigating macroevolutionary SD patterns. For the former, one typically collects phenotypic data on males and females among populations exploiting different habitats and then uses regression-type models to test how sex and habitat type are associated with the response phenotypic trait(s). In such studies, a significant contribution of the interaction term in explaining phenotypic variance across individuals indicates a variation of SD across habitats and suggests different ecomorphological responses in males and females. Further data analyses then seek to provide insight on the underlying biological mechanisms. By contrast, analyses of SD variation across species are typically conducted in a phylogenetic comparative framework, where species phenotypic data are compared in the light of the phylogenetic hypothesis of their evolutionary relationships (Harvey & Pagel, 1991). With this approach, phylogenetic history is explicitly incorporated into analytical procedures in the form of the phylogenetic covariance matrix (Felsenstein, 1985). Inferences about the influence of habitat use on phenotypic evolution are then made using phylogenetic generalized least squares (PGLS: Grafen, 1989; Rohlf, 2001) and/or by comparing the fit of different evolutionary models (Felsenstein, 1988; Butler & King, 2004).

From an inferential point of view, though, macroevolutionary analyses examining variation of the degree of SD in relation to some grouping factor (e.g. habitat) do not fully coincide with the procedure followed using

intraspecific data. Unlike what happens in individual-based intraspecific analyses, comparative modelling does not provide direct access to the underlying male and female trait variances, because the degree of sexual dimorphism itself is evaluated, rather than the original male–female trait values. The reason for this is that if sex were to be treated as a factor when examining macroevolutionary responses to habitat use, it would require two values per species (male and female phenotypes), whereas the phylogeny contains only one tip per species. Thus, the phylogenetic covariance matrix is incommensurate with the dimensionality of the phenotypic data if both sexes are included. As such, the only means of assessing whether both sexes respond differently to habitat variation – or variation in other traits of interest – at the macroevolutionary level is by treating SD as a trait and tracing its evolution on the phylogeny.

A caveat related to this macroevolutionary approach is the fact that SD is not – strictly speaking – a species trait, but rather an emergent property, which, as described above, depends on the balance of evolutionary influences on male and female phenotypes. For this reason, the comprehension of how SD varies across environments requires the explicit examination of phenotypic evolution in male and female traits. This is because variation in estimated model parameters across the sexes will be reflected in model parameters estimated for SD, thus crucially influencing evolutionary inferences. For instance, variation in the direction and strength of the evolutionary dynamics of male and female phenotypes may translate into different alternative macroevolutionary SD patterns (Fig. 1a). Conversely, apparently similar macroevolutionary SD patterns may emerge due to different combinations of underlying male and female processes of phenotypic evolution (Fig. 1b). Only a detailed examination of model parameters across male phenotypes, female phenotypes and SD will actually allow a correct evolutionary interpretation of the data.

Lizards have been extensively used as model organisms both for establishing the role of habitat use in shaping ecomorphological variation (e.g. Losos, 1990a, b; Garland & Losos, 1994; Vitt *et al.*, 1997; Melville & Swain, 2000; Collar *et al.*, 2010, 2011) and for understanding SD evolution (e.g. Butler *et al.*, 2000; Butler & Losos, 2002; Olsson *et al.*, 2002; Cox *et al.*, 2003; Butler & King, 2004). This aids evolutionary inference, by providing predictions on the expected mode of evolution with respect to potential effects of habitat use and to male–female differentiation. For instance, sexual size dimorphism has been associated to sexual selection on male body size in many lizard species, where larger males exhibit an evolutionary advantage for territory defence and mate acquisition (Stamps, 1983; Andersson, 1994; Cox *et al.*, 2007). Similarly, trunk length is known to be under fecundity selection in female



**Fig. 1** Hypothetical pattern of the evolution of the degree of sexual dimorphism (SD) across time (grey lines) with respect to the underlying pattern of phenotypic evolution in males (blue) and females (red) in a group with male-biased dimorphism. (a1): Trait mean value changes directionally across time, under the same rule for both sexes, resulting in a constant SD value. (a2): Trait mean value changes directionally across time, under different rules for both sexes, which causes variation across time in the degree of SD. (b1): Male mean trait value changes directionally across time, but female mean trait value does not. (b2): Male mean trait value is stable across time, but female mean trait value changes directionally. In both (b1) and (b2), a directional change in the degree of SD across time emerges.

lizards, as it determines the space available for egg storage and it may enhance progeny quality and/or quantity (Braña, 1996; Olsson *et al.*, 2002). Head size and shape also vary extensively in lizards and are functionally relevant for feeding, refuge and habitat use, as well as for competitive interactions and mating in males. Through associations with biting performance, head traits are thus potentially under the influence of both natural (Herrel *et al.*, 1996, 2001) and sexual (Husak *et al.*, 2006; Herrel *et al.*, 2007; Lailvaux & Irschick, 2007; Kaliontzopoulou *et al.*, 2012b) selection. Finally, limb length is tightly linked to locomotor performance, and it is differentially optimized in relation to predator escape and territory exploitation and defence in different structural habitats in many lizard groups (e.g. Losos, 1990a,b; Garland & Losos, 1994; Melville & Swain, 2000; Herrel *et al.*, 2002; Elstrott & Irschick, 2004; Tulli *et al.*, 2011).

Our objective in this study was to explore the macroevolutionary dynamics of phenotypic evolution in relation to habitat use in Iberian and North African *Podarcis* wall lizards in a phylogenetic comparative framework. Based on previous ecomorphological studies in lizards, we expect habitat use to mainly influence body size, head shape and relative limb length. However, which traits may exhibit a stronger association to habitat use, and whether this association may occur in unison, or

differ, between both sexes and consequently cause, or not, macroevolutionary variation in the degree of SD across habitats is difficult to predict for *Podarcis*. First, a lack of an evolutionary association between habitat use and locomotion-related morphological traits has been reported for lacertids at the family level (Vanhooydonck & Van Damme, 1999). Second, lizards of the genus *Podarcis* are not habitat specialists, but instead occupy a large variety of habitats (Arnold, 1987, 1998; Kaliontzopoulou *et al.*, 2010a). The Iberian and North African clade in particular consists of lineages which exhibit mainly parapatric distribution ranges (Carretero, 2008), such that habitat segregation due to coexistence is rare. Nevertheless, habitat use and geographic variation are known to influence body size and shape at the intra-specific level, where morphological responses differ between the sexes (Kaliontzopoulou *et al.*, 2010a,c), which suggests that environmental factors may have different effects on males and females. Finally, an examination of morphological diversity across all Iberian/North African *Podarcis* lineages suggested that the high variation observed in head height and limb length might be associated with habitat use (Kaliontzopoulou *et al.*, 2012a). Together, these studies imply that different body parts have evolved under different regimes in male and female *Podarcis*, and point to an important contribution of sex-specific morphological responses to

environmental variation in the evolution of phenotypic diversity. To infer whether this is the case, and examine which traits respond to habitat variation in this group of lizards, we compare different evolutionary models to explore whether and how the tempo and mode of phenotypic evolution vary across traits and between the sexes.

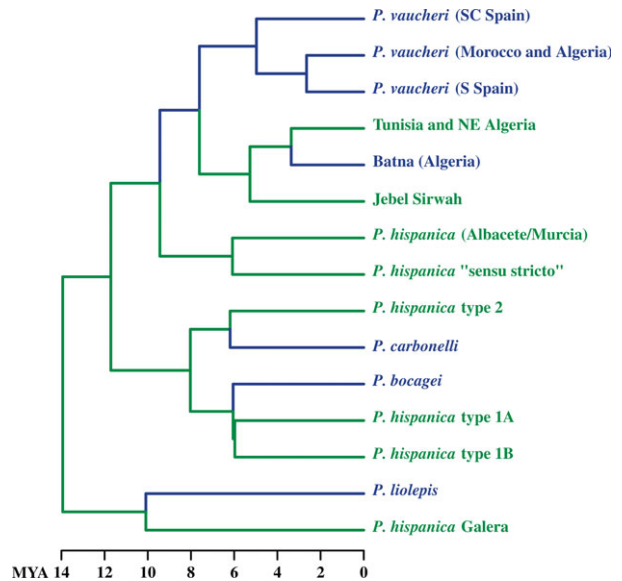
## Materials and methods

### Study organisms

Wall lizards of the genus *Podarcis* are a characteristic element of Mediterranean ecosystems and an emerging model in ecology and evolution (e.g. Calsbeek *et al.*, 2010; Camargo *et al.*, 2010; Runemark *et al.*, 2010; Piras *et al.*, 2011; Schulte *et al.*, 2011; Amaral *et al.*, 2012; Salvi *et al.*, 2013). The genus has a circum-Mediterranean distribution, ranging from the Iberian Peninsula to Turkey and from the south of Germany to the high Atlas mountain range in Morocco (Harris & Arnold, 1999). Despite intensive research, phylogenetic relationships among *Podarcis* species are not fully resolved (Harris *et al.*, 2005; Poulakakis *et al.*, 2005). However, four main, monophyletic groups with geographic coherence are supported by most molecular studies, including a Balkan, an Italian, a western insular and an Iberian/North African clade (Harris & Arnold, 1999; Harris *et al.*, 2005). Here, we focus on the westernmost clade of the genus (the Iberian/North African clade), for which a robust phylogenetic hypothesis is available. This clade occupies all the Iberian Peninsula, and in North Africa, it extends from Morocco, through Algeria, to north-eastern Tunisia (see Fig. 2 in Kaliontzopoulou *et al.*, 2011). It is considered a cryptic species complex, with 16 known mtDNA lineages (Kaliontzopoulou *et al.*, 2011) which are supported by both morphological (Kaliontzopoulou *et al.*, 2012a) and nuclear (Pinho *et al.*, 2008) data.

### Morphological data

We examined a total of 2453 specimens, captured across 75 localities distributed throughout the Iberian Peninsula and North Africa and representing 15 of the 16 mtDNA lineages of the Iberian/North African clade of *Podarcis* (Kaliontzopoulou *et al.*, 2011). We sampled multiple localities per lineage to include in our sample a full representation of individual variation. We only considered adult specimens, identified based on minimum adult snout-vent length for lineages for which detailed studies on reproductive biology are available (Galán, 1996, 2003; Carretero *et al.*, 2006; Kaliontzopoulou *et al.*, 2006). When information on sexual maturity was not available, we identified adult individuals by the presence of copulatory marks and eggs in females and by the presence of secondary sexual traits in males.



**Fig. 2** Time-dated molecular phylogeny of the Iberian and North African clade of *Podarcis* wall lizards obtained based on the calibration of node ages of the most recent mtDNA phylogenetic hypothesis for the group (Kaliontzopoulou *et al.*, 2011). Habitat use reconstruction obtained through ML is indicated in different colours (green: saxicolous; blue: generalist).

For each individual, we quantified the following linear biometric traits, measured to the closest 0.01 mm using electronic calipers: snout-vent length (SVL), trunk length (TRL), head length (HL), head width (HW), head height (HH), forelimb length (FLL) and hindlimb length (HLL; all data from Kaliontzopoulou *et al.*, 2012a). These traits were chosen because they are relevant for different functions, and as such, they are expected to evolve under different selective mechanisms (see above). We used SVL as a representation of total body size. All variables were log-transformed prior to statistical analyses to better approximate a normal distribution, buffer the effect of trait scale on variable variance and facilitate SD comparisons.

### Species data and phylogenetic relationships

We used phylogenetic comparative methods to test hypotheses concerning the tempo and mode of phenotypic evolution in *Podarcis*. Our goal was to examine evolutionary responses to habitat use at the macroevolutionary level, considering male phenotypes, female phenotypes and the degree of SD. Because of this, we performed three sets of parallel comparative analyses: the first on male trait values, the second on female trait values and the third on the degree of SD. For all analyses, we first calculated a mean male and female value for each trait within each mtDNA lineage. Because allometry of different body parts is known to be a

major proximate determinant of adult SD in lizards (Braña, 1996; Cox *et al.*, 2007; Kaliontzopoulou *et al.*, 2008b, 2010b; Urošević *et al.*, 2012; Sanger *et al.*, 2013), we filtered our data to obtain an estimate of maximal adult male and female body size for each mtDNA lineage. This minimized the effects of random sampling of individuals on the macroevolutionary patterns observed and reduced the potential noise in our data due to allometric variation across lineages. For this purpose, we used the ten largest male and the ten largest female individuals encountered across the sample available for each mtDNA lineage, which provide us with an approximation of asymptotic body size, and corresponding body shape, for each evolutionary group considered.

Although size and shape SD have been frequently examined from a multivariate perspective, combining several traits (e.g. Butler & Losos, 2002), here we preferred to restrict our analyses to single-trait comparisons. The decision for evaluating patterns in each trait individually was based on several biological reasons. First, because each trait is involved in different ecological and social functions, we were interested in examining them separately to establish links between macroevolutionary patterns in male and female phenotypes and those observed for SD in each trait. Second, we were interested in conducting comparisons across traits, which at present can only be achieved for univariate data. As such, the degree of SD for each trait and lineage was represented by the difference between log-transformed male and female values, corresponding to the ratio between male and female trait values for the raw data (Smith, 1999). Size SD was represented by the difference between males and females in SVL. Trait shape SD was obtained as the difference between males and females in the logarithm of size-corrected traits, after correcting for size effects through phylogenetic regression of each trait on SVL.

Phylogenetic relationships among taxa were found using the most recent mtDNA phylogenetic hypothesis available for the Iberian/North African clade of *Podarcis* wall lizards, inferred based on 2291 bp from five mitochondrial regions (Kaliontzopoulou *et al.*, 2011). This topology was subjected to a semiparametric penalized likelihood procedure (Sanderson, 2002), as implemented in the *chronopl* function of ape R-package (Paradis *et al.*, 2004), to obtain a time-dated chronogram. Calibration points for this analysis were the divergence time estimates obtained based on a compiled data set including Iberian, North African and Greek *Podarcis* species, and considering the end of the Messinian Salinity Crisis as a reference point (INAG calibration scheme, Table 2 in Kaliontzopoulou *et al.*, 2011). Because the 'Azazga' lineage was not present in our phenotypic data set, this taxon was dropped from the chronogram (Fig. 2).

### Habitat use

To investigate whether habitat use has influenced morphological evolution, we classified mtDNA lineages into one of two habitat types. Iberian/North African *Podarcis* constitute the most saxicolous clade within the genus (Arnold, 1987), which means that they all show a preference for walls, rocks and other rocky surfaces. Consequently, variation in habitat use in the Iberian/North African clade can be found in the frequency with which different lineages exploit other types of habitats. Some forms, such as *P. hispanica* type 1A, are highly saxicolous, inhabiting exclusively large rocks or human-constructed walls (Kaliontzopoulou *et al.*, 2012b). Others, such as *P. bocagei*, exhibit more generalistic habits and are frequently encountered in other types of habitats, including dunes, sparse vegetation and the ground of forested areas (Kaliontzopoulou *et al.*, 2010a). Based on the few existing bibliographic data and, mainly, on our own observations during fieldwork, we classified as generalists seven of the 15 lineages, comprising *P. vaucheri* from south-central Spain, *P. vaucheri* from Morocco and Algeria, and *P. vaucheri* from southern Spain, as well as *P. hispanica* from Batna, Algeria, *P. bocagei*, *P. carbonelli* and *P. liol-epis*. Conversely, the eight remaining lineages were classified as saxicolous, including *P. hispanica* from Tunisia and Algeria, *P. hispanica* from Jbel Siroua, *P. hispanica* from Albacete and Murcia, *P. hispanica sensu stricto*, *P. hispanica* type 2, *P. hispanica* type 1A, *P. hispanica* type 1B and *P. hispanica* Galera (Fig. 2). Based on this classification, we inferred the ancestral state of habitat at the internal nodes of the phylogeny using maximum likelihood as implemented in the *ace* function of R-package ape (Paradis *et al.*, 2004).

### Phylogenetic comparative analyses

Because there is considerable size variation among species, we accounted for body size variation in species means by applying a phylogenetic size correction of each morphological trait on SVL (Revell, 2009). Phylogenetic size correction was performed using the *phyl.re-sid* function of the phyttools R-package (Revell, 2012). We then tested whether lineages occupying different habitat types differ morphologically for body size and shape, whereas accounting for phylogenetic relationships, using phylogenetic generalized least squares (Rohlf, 2001). By implementing this analysis on males, females and the degree of SD, we could infer how the two sexes respond morphologically to habitat variation and examine how differences in their responses may cause variation in the degree of SD across taxa.

To investigate the evolutionary processes through which habitat use influences the degree of SD, and link such variation across taxa to the underlying male and female mechanisms of phenotypic evolution, we used

phylogenetic comparative modelling to contrast different evolutionary hypotheses. For instance, habitat use may trigger differences in the pace of phenotypic diversification (Collar *et al.*, 2010, 2011; Rabosky *et al.*, 2014). That is, lineages that use a wider ecological niche (i.e. generalists) may also exhibit increased phenotypic variance, which would be diagnosed as a higher evolutionary rate in those lineages. Similarly, adaptive evolution towards one or more phenotypic optima can be identified by examining the fit of evolutionary models with a selective component. To test these hypotheses in our data set, we fit four models of phenotypic change on the phylogeny, for each male, female and SD trait separately. The first model was a single-rate Brownian motion (BM: Edwards & Cavalli-Sforza, 1964; Felsenstein, 1985, 1988; Harvey & Pagel, 1991), which is generally considered to represent neutral phenotypic evolution by drift, or a balance between drift and mutation (Felsenstein, 1985, 1988; Hansen & Martins, 1996), where phenotypic variance accumulates with the same rate across all lineages. The second model was a BM with separate evolutionary rates for each habitat type, and it was implemented using the noncensored test proposed by O'Meara *et al.* (2006). The third model represented an Ornstein–Uhlenbeck (OU) process with a single adaptive optimum for all lineages (OU1); under this hypothesis, directional selection drives the means of all lineages towards the same value (Hansen & Martins, 1996; Butler & King 2004). The last model considered represented an OU process with different phenotypic optima for each habitat type (OUM); under this scenario, phenotypic evolution shows signs of diversifying selection, where the phenotypes of species belonging to each habitat group evolve towards different optimal values (Hansen & Martins, 1996; Butler & King 2004; Beaulieu *et al.*, 2012). All evolutionary models were fit using the OUwie R-package (Beaulieu & O'Meara, 2012), and their goodness-of-fit to the data was compared using the Akaike information criterion (with a correction for small sample size, AICc) and likelihood ratio tests (LRTs, for pairs of nested models). By fitting these models to male traits, female traits and the degree of SD, we could infer how SD has evolved as a response to habitat use, and link the evolution of SD with the dynamics of phenotypic evolution of males and females.

Because both PGLS and model comparison revealed variation in phylogenetic variance across traits and between the sexes, we specifically focused on the pace of phenotypic evolution by testing for variation in evolutionary rates across traits and between the sexes. This provided us with a means of evaluating whether the accumulation of phenotypic diversity varies for different traits, as may be predicted if selective influences vary across traits. Under the same reasoning, evolutionary rates may vary across the sexes for a specific trait, if phenotypic diversity across lineages accumulates faster

in one sex than in the other. To test these hypotheses, we used a recently proposed maximum likelihood procedure (Adams, 2013) to compare a single-rate model to a model encompassing different rates for each trait. This analysis was implemented in a pairwise manner, to examine variation in evolutionary rates for a single phenotypic trait across the sexes and to test for differences in evolutionary rates between pairs of traits in females, males and SD separately.

All statistical analyses were conducted using the R language for statistical programming (R Core Team, 2013). Phenotypic data, the ultrametric phylogeny used, and habitat type distribution across phylogeny nodes are available from the Dryad Digital Repository: doi: 10.5061/dryad.d5jc3.

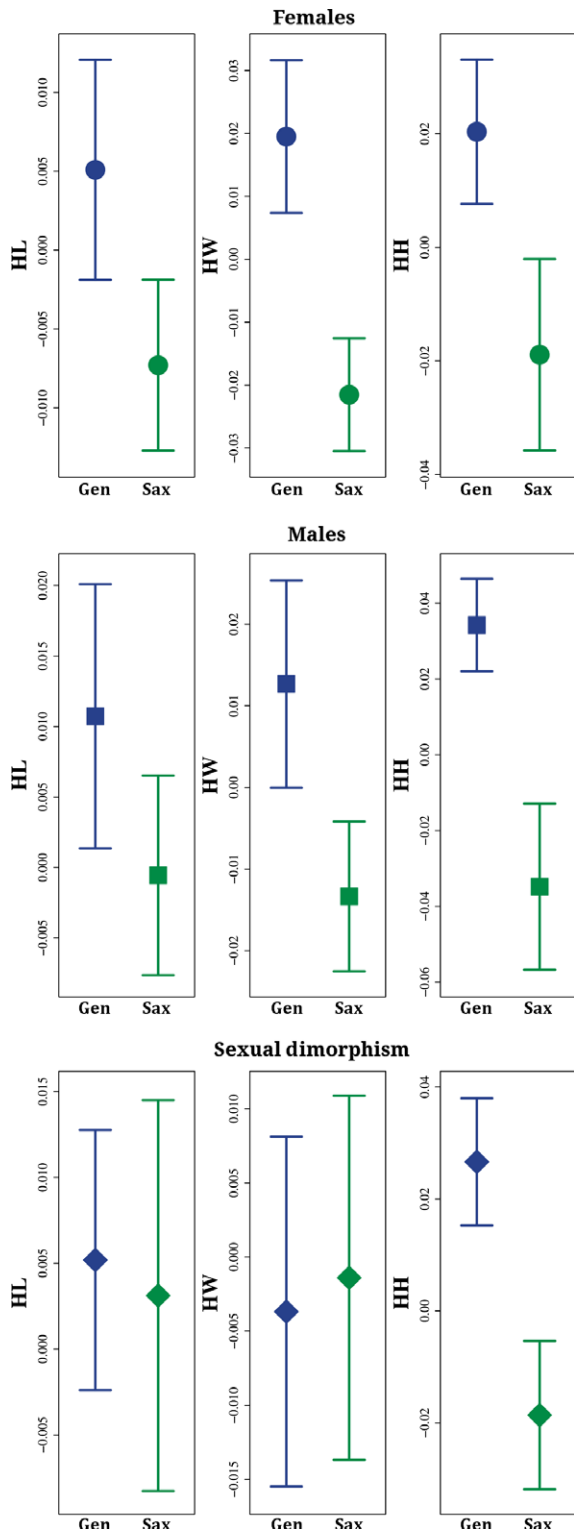
## Results

Phylogenetic ANOVA revealed that *Podarcis* lizards with different habitat preferences differ in relative head dimensions, but not in body size, relative trunk or relative limb length (Table 1). However, habitat use influenced different traits in each sex: females of generalist lineages exhibited wider heads compared to saxicolous ones, whereas males of generalist lineages had higher heads in comparison to saxicolous ones (Table 1; Fig. 3). These differences across the sexes translated into a difference between habitats in the degree of head height SD, where generalist lineages were more dimorphic than saxicolous ones (Table 1, Fig. 3).

Model comparison revealed that the effect of habitat use on phenotypic evolution varied across traits, where differences in male vs. female evolutionary dynamics translated into varying macroevolutionary patterns of SD (Tables 2 and 3). The best-fit model for total body size (SVL) was a simple BM for both males and females, receiving the lowest AICc scores, highest AIC weights (about 0.5 in both sexes), and with a likelihood score that was not significantly lower than that of more complex models (Tables 2 and 3). By contrast, a two-rate BM model was best supported for size SD, which received the highest AIC weight ( $\approx 0.7$ ), exhibited a

**Table 1** Results of phylogenetic ANOVA considering the effect of habitat type on lineage mean values of body size (SVL) and size-corrected traits. Significant p-values are marked in bold.

|                   | Females |             | Males |             | SD   |             |
|-------------------|---------|-------------|-------|-------------|------|-------------|
|                   | F       | P           | F     | P           | F    | P           |
| Snout-vent length | 1.01    | 0.34        | 0.99  | 0.33        | 0.05 | 0.82        |
| Trunk length      | 0.03    | 0.88        | 0.87  | 0.32        | 0.69 | 0.42        |
| Head length       | 1.82    | 0.19        | 0.86  | 0.35        | 0.02 | 0.89        |
| Head width        | 6.90    | <b>0.02</b> | 2.58  | 0.12        | 0.02 | 0.91        |
| Head height       | 2.97    | 0.10        | 6.30  | <b>0.02</b> | 5.89 | <b>0.04</b> |
| Forelimb length   | 0.03    | 0.86        | 0.16  | 0.71        | 0.30 | 0.58        |
| Hindlimb length   | 0.00    | 0.97        | 0.03  | 0.86        | 0.03 | 0.86        |



**Fig. 3** Least squares means of size-corrected head length (HL), head width (HW) and head height (HH) in the two habitat types considered (green: saxicolous; blue: generalist) for females, males and SD. Vertical bars denote 95% confidence intervals.

significantly higher likelihood than a simple BM and indicated that size SD evolved about 10 times faster in generalist than in saxicolous lineages (Table 2, Table S1). A similar pattern was observed for size-corrected trunk length (TRL). For this trait, an OU model with a single phenotypic optimum was best supported for both sexes (OU1; 0.743 and 0.599 of AIC weight for males and females respectively, Table 2), exhibiting a significantly higher likelihood than a simple BM model (Table S1). Note that the phylogenetic half-life parameters ( $t_{1/2}$ , Hansen, 1997) estimated for both males and females were very low, indicating strong selection for this trait in both sexes (Table 2). Although parameter estimates may be somewhat unstable in this case, as indicated by unrealistically high evolutionary rates inferred for TRL, the estimated stochastic variance ( $\sigma^2/2*\alpha$ ) approximates trait variance in both sexes. This implies that there may not be sufficient information in our data set to accurately estimate  $\sigma^2$  and  $\alpha$  independently. Nevertheless, strong stabilizing selection on male and female TRL is supported by the data (Hansen, 1997). By contrast, the best-fit model for size-corrected trunk length SD was again a two-rate BM (AICw = 0.557, Table 2), where trunk length SD evolved more than five times faster in generalists, as compared to saxicolous lineages.

Contrary to what was observed for body size and trunk length, the phenotypic evolution of head dimensions exhibited signs of diversifying selection due to habitat use (Table 3). For size-corrected head length (HL), OU1 was the model that received the highest support in females (AICw = 0.70), whereas a simple BM was the best-fit model in males (AICw = 0.66). This translated into stabilizing selection for head length SD (OU1: AICw = 0.7; Table 2), mirroring the hypothetical evolutionary scenario of Fig. 1b2. By contrast, a two-optimum OU model (OUM) was supported for size-corrected head width (HW) in both sexes, exhibiting high (0.74) and moderate (0.31) AIC weights in females and males, correspondingly, and a significantly higher likelihood than BM1 or OU1 in both sexes (Table 2, Table S1). However, head width SD evolution was better described by a single-peak OU model (AICw = 0.74; Table 2). An almost inverse evolutionary pattern was observed in the case of size-corrected head height (HH). Here, a single-optimum OU model (OU1) was best supported for female HH, despite a moderate AIC weight (0.39) and a high likelihood ratio compared to the OUM model (Table S1). By contrast, the two-optimum OUM model was best supported male HH and the degree of SD observed in this trait (Table 3). Males of generalist lineages evolved towards higher HH values than saxicolous ones, which, combined to a uniform evolution across habitat types in females, results in an increased phenotypic optimum for SD in this trait (Table 2).

In contrast to ecomorphological predictions, we found no evidence for an evolutionary effect of habitat

**Table 2** Parameter estimates and model fitting for the phenotypic traits examined in females, males and the degree of SD in Iberian and North African *Podarcis* wall lizards. The best-fit model (inferred through examination of both AICc weights and likelihood ratio tests, see Table S1) is highlighted in bold letter. k: number of parameters in the model, AICc: Akaike information criterion for small sample sizes, AICw: Akaike weight,  $\sigma^2$ : estimated evolutionary rate,  $t_{1/2}$ : phylogenetic half-life ( $\ln(2)/\alpha$ );  $\beta$ : estimated optimum for OU models. Note that for the two-rate model (BMS), the relative rate between saxicolous and generalists ( $\sigma^2_{\text{sax}}/\sigma^2_{\text{gen}}$ ) is given. Similarly, for the two-optimum model (OUM), the difference in optima between saxicolous and generalists ( $\beta_{\text{sax}} - \beta_{\text{gen}}$ ) is given. Note that the phylogeny was rescaled to unit total tree length. SVL: snout-vent length, TRL: trunk length, HL: head length, HW: head width, HH: head height, FLL: forelimb length, HLL: hindlimb length.

| Trait | Model | k | Females       |              |              |              |               | Males         |              |              |              |               | SD            |              |              |              |               |
|-------|-------|---|---------------|--------------|--------------|--------------|---------------|---------------|--------------|--------------|--------------|---------------|---------------|--------------|--------------|--------------|---------------|
|       |       |   | AICc          | AICw         | $\sigma^2$   | $t_{1/2}$    | $\beta$       | AICc          | AICw         | $\sigma^2$   | $t_{1/2}$    | $\beta$       | AICc          | AICw         | $\sigma^2$   | $t_{1/2}$    | $\beta$       |
| SVL   | BM    | 2 | <b>-13.25</b> | <b>0.511</b> | <b>0.026</b> | –            | –             | <b>-10.73</b> | <b>0.519</b> | <b>0.031</b> | –            | –             | -47.39        | 0.120        | 0.003        | –            | –             |
|       | BMS   | 3 | -10.95        | 0.162        | 2.358        | –            | –             | -7.66         | 0.112        | 1.294        | –            | –             | <b>-50.92</b> | <b>0.698</b> | <b>0.097</b> | –            | –             |
|       | OU1   | 4 | -11.85        | 0.254        | 0.117        | 0.183        | 4.032         | -9.57         | 0.291        | 0.448        | 0.055        | 4.063         | -47.94        | 0.158        | 0.193        | 0.010        | 0.029         |
|       | OUM   | 5 | -9.37         | 0.073        | 0.242        | 0.081        | -0.080        | -6.96         | 0.079        | 0.396        | 0.058        | -0.079        | -44.19        | 0.024        | 0.635        | 0.003        | -0.005        |
| TRL   | BM    | 2 | -54.47        | 0.055        | 0.002        | –            | –             | -64.24        | 0.191        | 0.001        | –            | –             | -61.64        | 0.246        | 0.001        | –            | –             |
|       | BMS   | 3 | -55.46        | 0.090        | 0.245        | –            | –             | -61.47        | 0.048        | 0.586        | –            | –             | <b>-63.27</b> | <b>0.557</b> | <b>0.190</b> | –            | –             |
|       | OU1   | 4 | <b>-59.69</b> | <b>0.743</b> | <b>0.116</b> | <b>0.008</b> | <b>0.008</b>  | <b>-66.53</b> | <b>0.599</b> | <b>0.006</b> | <b>0.092</b> | <b>-0.001</b> | -60.74        | 0.157        | 0.003        | 0.279        | -0.006        |
|       | OUM   | 5 | -55.91        | 0.112        | 0.301        | 0.003        | 0.003         | -63.93        | 0.163        | 0.004        | 0.123        | 0.014         | -58.03        | 0.041        | 0.003        | 0.237        | 0.020         |
| HL    | BM    | 2 | -62.70        | 0.015        | 0.001        | –            | –             | <b>-67.87</b> | <b>0.661</b> | <b>0.001</b> | –            | –             | -54.77        | 0.150        | 0.002        | –            | –             |
|       | BMS   | 3 | -60.91        | 0.006        | 0.291        | –            | –             | -64.70        | 0.136        | 0.843        | –            | –             | -51.81        | 0.034        | 1.499        | –            | –             |
|       | OU1   | 4 | <b>-70.41</b> | <b>0.701</b> | <b>0.056</b> | <b>0.008</b> | <b>-0.002</b> | -64.98        | 0.156        | 0.001        | 0.719        | 0.001         | <b>-57.87</b> | <b>0.709</b> | <b>0.025</b> | <b>0.039</b> | <b>0.004</b>  |
|       | OUM   | 5 | -68.56        | 0.278        | 0.145        | 0.003        | -0.012        | -62.61        | 0.048        | 0.001        | 0.523        | -0.025        | -54.09        | 0.107        | 0.016        | 0.061        | -0.003        |
| HW    | BM    | 2 | -46.90        | 0.043        | 0.003        | –            | –             | -53.45        | 0.299        | 0.002        | –            | –             | -48.12        | 0.105        | 0.003        | –            | –             |
|       | BMS   | 3 | -44.51        | 0.013        | 0.192        | –            | –             | -52.14        | 0.155        | 0.313        | –            | –             | -46.61        | 0.049        | 5.858        | –            | –             |
|       | OU1   | 4 | -50.03        | 0.205        | 0.030        | 0.056        | -0.002        | -52.97        | 0.235        | 0.005        | 0.267        | -0.002        | <b>-52.02</b> | <b>0.736</b> | <b>0.165</b> | <b>0.009</b> | <b>-0.002</b> |
|       | OUM   | 5 | <b>-52.60</b> | <b>0.740</b> | <b>0.397</b> | <b>0.003</b> | <b>-0.041</b> | <b>-53.54</b> | <b>0.312</b> | <b>0.005</b> | <b>0.229</b> | <b>-0.048</b> | -48.22        | 0.110        | 0.628        | 0.002        | 0.002         |
| HH    | BM    | 2 | -40.42        | 0.176        | 0.004        | –            | –             | -37.97        | 0.390        | 0.005        | –            | –             | -44.71        | 0.097        | 0.003        | –            | –             |
|       | BMS   | 3 | -39.52        | 0.112        | 14.016       | –            | –             | -35.21        | 0.098        | 3.734        | –            | –             | -41.57        | 0.020        | 0.846        | –            | –             |
|       | OU1   | 4 | <b>-42.01</b> | <b>0.390</b> | <b>0.053</b> | <b>0.054</b> | <b>-0.001</b> | -35.37        | 0.106        | 0.009        | 0.635        | -0.002        | -45.56        | 0.148        | 0.016        | 0.138        | 0.002         |
|       | OUM   | 5 | -41.63        | 0.322        | 0.034        | 0.067        | -0.044        | <b>-38.06</b> | <b>0.407</b> | <b>0.007</b> | <b>0.435</b> | <b>-0.126</b> | <b>-48.76</b> | <b>0.735</b> | <b>0.010</b> | <b>0.148</b> | <b>-0.063</b> |
| FLL   | BM    | 2 | -44.32        | 0.068        | 0.003        | –            | –             | <b>-43.91</b> | <b>0.520</b> | <b>0.003</b> | –            | –             | <b>-57.80</b> | <b>0.328</b> | <b>0.001</b> | –            | –             |
|       | BMS   | 3 | -42.95        | 0.035        | 0.354        | –            | –             | -40.73        | 0.106        | 1.110        | –            | –             | -57.31        | 0.257        | 0.210        | –            | –             |
|       | OU1   | 4 | <b>-49.19</b> | <b>0.780</b> | <b>0.222</b> | <b>0.008</b> | <b>-0.002</b> | -42.87        | 0.309        | 0.010        | 0.291        | -0.001        | -57.85        | 0.336        | 0.004        | 0.236        | 0.001         |
|       | OUM   | 5 | -45.40        | 0.117        | 0.597        | 0.003        | -0.003        | -39.72        | 0.064        | 0.010        | 0.270        | -0.029        | -54.96        | 0.079        | 0.004        | 0.216        | -0.019        |
| HLL   | BM    | 2 | -39.23        | 0.049        | 0.005        | –            | –             | -41.78        | 0.250        | 0.004        | –            | –             | -60.89        | 0.086        | 0.001        | –            | –             |
|       | BMS   | 3 | -36.97        | 0.016        | 0.502        | –            | –             | -38.62        | 0.051        | 1.132        | –            | –             | -61.78        | 0.134        | 0.222        | –            | –             |
|       | OU1   | 4 | <b>-44.84</b> | <b>0.814</b> | <b>0.289</b> | <b>0.008</b> | <b>0.002</b>  | <b>-43.53</b> | <b>0.599</b> | <b>0.020</b> | <b>0.130</b> | <b>0.004</b>  | <b>-64.97</b> | <b>0.661</b> | <b>0.005</b> | <b>0.114</b> | <b>0.003</b>  |
|       | OUM   | 5 | -41.02        | 0.121        | 0.794        | 0.003        | -0.001        | -39.94        | 0.100        | 0.017        | 0.153        | -0.014        | -61.53        | 0.119        | 0.005        | 0.132        | -0.008        |

**Table 3** Best-fit evolutionary model for each trait in females, males and SD, based on likelihood ratio tests (see also Table 2, Table S1). BM1: single-rate Brownian motion; BMS: Brownian motion with separate rates for each habitat type; OU1: single-optimum Ornstein–Uhlenbeck; OUM: Ornstein–Uhlenbeck with different optima for each habitat type.

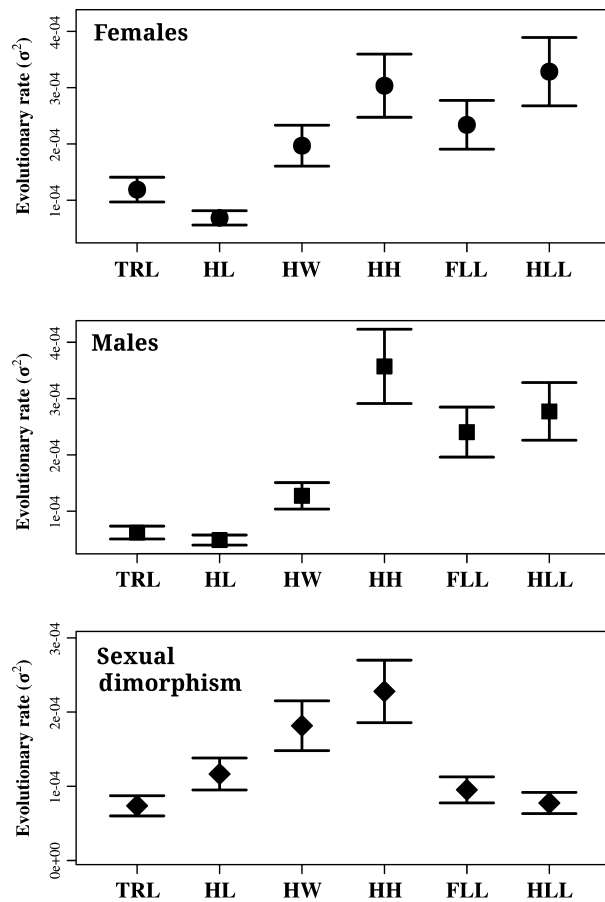
|     | Females | Males | SD  |
|-----|---------|-------|-----|
| SVL | BM1     | BM1   | BMS |
| TRL | OU1     | OU1   | BMS |
| HL  | OU1     | BM1   | OU1 |
| HW  | OUM     | OUM   | OU1 |
| HH  | OU1     | OUM   | OUM |
| FLL | OU1     | BM1   | BM1 |
| HLL | OU1     | OU1   | OU1 |

use on limb length in either males, females or the degree of SD (Table 3). Variation across lineages in size-corrected forelimb length (FLL) was best explained

by a single-optimum OU model (OU1) in females (AICw = 0.78), whereas a simple BM was the best supported model for male FLL and the degree of SD in this trait (Table 2). Signs of stabilizing selection were found for size-corrected hindlimb length (HLL) in both sexes, for which OU1 was also the best supported model.

The comparison of evolutionary rates between males and females indicated that phenotypic traits evolve at the same pace in both sexes, where the two-rate model never exhibited a significantly higher likelihood than the single-rate model (Fig. 4; Table S2). By contrast, evolutionary rates varied extensively among traits, particularly in males (Table 4; Table S3). Head length was the slowest evolving trait in both sexes (Table 4; Fig. 4). In males, two blocks of traits emerged, considering evolutionary rates: trunk length, head length and head width evolved at a slower pace, whereas head height and limb length exhibited higher evolutionary





**Fig. 4** Evolutionary rates for different traits in females, males and SD. Vertical bars denote 95% confidence intervals of rate estimators, calculated through the Hessian matrix of the likelihood function. TRL: trunk length, HL: head length, HW: head width, height HH: head, FLL: forelimb length, HLL: hindlimb length.

rates (Table 4; Fig. 4). Rate variation across traits was less prominent for the degree of SD, where we only found evidence of faster evolution for head height SD, at least when compared to trunk length and hindlimb length SD (Table 4; Fig. 4).

## Discussion

Understanding how male and female phenotypes evolutionarily respond to environmental factors is essential for our comprehension of the processes underlying the generation of phenotypic diversity. Our results suggest that males and females of Iberian and North African wall lizards have globally diversified under similar, but not identical, processes. Indeed, the tempo of phenotypic evolution was uniform across the sexes for all traits studied, whereas the same was the case for evolutionary mode in most cases. Contrary to predictions made under the ecomorphological paradigm, habitat

**Table 4** Relative evolutionary rates observed between pairs of traits (below the diagonal; calculated as  $\sigma_{\text{trait1}}^2/\sigma_{\text{trait2}}^2$ ) and p-value of the LRT between a two-rate and a single-rate model (above the diagonal). Significant p-values and corresponding relative rates are marked in bold. TRL: trunk length, HL: head length, HW: head width, HH: head height, FLL: forelimb length, HLL: hindlimb length. See Table S2 for detailed model statistics.

| Females |             | Trait 2 |             |             |             |             |             |
|---------|-------------|---------|-------------|-------------|-------------|-------------|-------------|
| Trait 1 |             | TRL     | HL          | HW          | HH          | FLL         | HLL         |
| TRL     |             |         | 0.29        | 0.33        | 0.07        | 0.19        | 0.05        |
| HL      | 0.58        |         | <b>0.05</b> | <b>0.01</b> | <b>0.02</b> | <b>0.00</b> | <b>0.00</b> |
| HW      | 1.66        |         | <b>2.87</b> |             | 0.40        | 0.74        | 0.32        |
| HH      | 2.55        |         | <b>4.42</b> | 1.54        |             | 0.62        | 0.88        |
| FLL     | 1.97        |         | <b>3.41</b> | 1.19        | 0.77        |             | 0.51        |
| HLL     | 2.76        |         | <b>4.78</b> | 1.67        | 1.08        | 0.65        |             |
| Males   |             | Trait 2 |             |             |             |             |             |
| Trait 1 |             | TRL     | HL          | HW          | HH          | FLL         | HLL         |
| TRL     |             |         | 0.64        | 0.17        | <b>0.00</b> | <b>0.01</b> | <b>0.01</b> |
| HL      | 0.79        |         |             | 0.07        | <b>0.00</b> | <b>0.00</b> | <b>0.00</b> |
| HW      | 2.05        |         | 2.61        |             | <b>0.05</b> | 0.22        | 0.14        |
| HH      | <b>5.76</b> |         | <b>7.34</b> | <b>2.81</b> |             | 0.44        | 0.62        |
| FLL     | <b>3.88</b> |         | <b>4.94</b> | 1.89        | 1.49        |             | 0.78        |
| HLL     | <b>4.47</b> |         | <b>5.69</b> | 2.18        | 0.78        | 1.15        |             |
| SD      |             | Trait 2 |             |             |             |             |             |
| Trait 1 |             | TRL     | HL          | HW          | HH          | FLL         | HLL         |
| TRL     |             |         | 0.38        | 0.09        | <b>0.03</b> | 0.62        | 0.92        |
| HL      | 1.58        |         |             | 0.39        | 0.20        | 0.70        | 0.43        |
| HW      | 2.46        |         | 1.56        |             | 0.66        | 0.22        | 0.10        |
| HH      | <b>3.09</b> |         | 1.96        | 1.25        |             | 0.10        | <b>0.04</b> |
| FLL     | 1.29        |         | 0.82        | 0.52        | 2.39        |             | 0.69        |
| HLL     | 1.05        |         | 0.66        | 0.43        | <b>0.34</b> | 0.81        |             |

use does not seem to have influenced the evolution of limb length in either males or females of Iberian and North African *Podarcis*. By contrast, habitat use is an important determinant of macroevolutionary variation in head shape, in accordance with observations in other lizard groups. Despite the general concordance in evolutionary patterns across the sexes, however, the analyses conducted indicate that even small differences in the evolutionary dynamics of male and female phenotypes can have a marked impact on macroevolutionary patterns of SD. Together, the results obtained here provide a different perspective on how habitat use influences male and female phenotypic evolution in lizards and have important implications for our comprehension of the evolution of sexual dimorphism, both from an organismal and conceptual perspective.

## Effects of habitat on phenotypic evolution

Habitat use is a major factor in the evolution of phenotypic diversity of many lizards, where locomotor performance has been documented as the main mediator of this link (Garland & Losos, 1994). Our analyses indicate an association between habitat use and macroevolutionary phenotypic patterns in Iberian and North

African wall lizards, but this association is apparently not linked to locomotor performance in this system, as we did not detect habitat-related macroevolutionary variation in traits involved in locomotor performance (i.e. total body size, fore and hindlimb length, trunk length; Table 1). Indeed, total body size and limb length of both males and females are best described by either a BM or a single-peak OU evolutionary model (Table 3). Although this result contradicts predictions of the ecomorphological paradigm and is in discordance with previous results in other lizard groups, it may be explained whether we take into consideration the habitat preferences of the species in question. Indeed, as mentioned before, Iberian and North African *Podarcis* exploit different habitats with different frequencies, but lack the extreme specializations observed in other lizard groups. For instance, major habitat shifts such as transition to grass swimming or branch climbing are absent among wall lizards. As such, lineages of this group may have preserved an 'all-purpose' locomotor morphology, which allows them to perform equally well under different ecological conditions. Such a hypothesis may also be supported by the observation that different locomotor capacities do not seem to trade off in this family, as may be expected due to morphological specialization for a certain type of locomotion (Van Damme *et al.*, 1997; Vanhooydonck & Van Damme, 2001). Indeed, preliminary data on two coexisting species (i.e. *P. bocagei* and *P. hispanica* type 1A; V. Gomes, M. A. Carretero & A. Kaliontzopoulou, unpublished data) reveal that the morphology–locomotion–habitat link may not be as evident in this group as it is in other lizards. Confirming this hypothesis would require the direct quantification of locomotor performance in the lineages examined here and its examination in the light of the evolutionary history of the group.

Instead of being related to body size and limb length, then, the association between habitat and morphology in Iberian and North African wall lizards appears restricted to head dimensions. A comparison of lineage means while accounting for the expected covariance due to shared evolutionary history revealed significant differences between saxicolous and generalist lizards of both sexes in head dimensions (Table 1). In addition, we found that an OU model with different optima for each habitat type fit the data better than simpler evolutionary models for some traits (Table 3), lending support to a hypothesis of adaptive evolution of head shape as a response to habitat use variation in Iberian and North African wall lizards. This evolutionary pattern is most probably related to physical constraints imposed by refuge use, commonly observed in rock-dwelling lizards (Revell *et al.*, 2007). As is also the case in other lizard groups (Vitt *et al.*, 1997), saxicolous Iberian and North African *Podarcis*, which use small rock crevices and holes to hide from predators, exhibited significantly flatter and narrower heads and evolved

towards lower optima for these head dimensions than those with more generalist habitat preferences (Table 2; Fig. 3). Although our study encompasses a relatively short evolutionary period (i.e. between 9.44 and 13.94 MY depending on the calibration method used, Kaliontzopoulou *et al.*, 2011), such a pattern seems evolutionarily repeatable in lacertids, as it has also been reported at the intraspecific (Kaliontzopoulou *et al.*, 2010a), genus (Urošević *et al.*, 2012) and family (Vanhooydonck & Van Damme, 1999) levels.

The difference observed across traits when considering macroevolutionary morphological responses to habitat use may also be associated to the escape tactics used by wall lizards. Among the ecological tasks for which locomotor performance – and associated morphological traits – is relevant, escape from predators is known to constitute an important selective pressure (Husak & Fox, 2006). Despite varying in microhabitat preferences, wall lizards generally inhabit areas with at least some complexity in terms of structural habitat, with an increased availability of refuges, and they are scarcely found in completely open areas such as sand dunes lacking vegetation (Arnold, 1987, 1998). As a result, they rely more on hiding than on long-distance speed running when eluding predators. Indeed, they usually remain in a relatively short distance from their refuges, to which they flee when threatened (Amo *et al.*, 2003; Diego-Rasilla, 2003). This kind of antipredatory behaviour may yield mechanical constraints related to refuge use more relevant than locomotor performance, resulting in a higher evolutionary pressure on head dimensions than on relative limb length.

Interestingly, our results indicate that although habitat use drives the evolution of head shape in Iberian and North African *Podarcis*, there is no evidence that it has caused a direct modification of diversification rates in this group. An effect of habitat use on diversification rates has been recently reported in some lizard groups (e.g. Agamidae: Collar *et al.*, 2010; *Varanus*: Collar *et al.*, 2011; Scincidae: Rabosky *et al.*, 2014), although along larger evolutionary time scales than those investigated here, and it would be a reasonable hypothesis for our study system, due to the classification of habitat variation. In fact, the 'generalist' representatives of this group by definition utilize a wider variety of structural habitats, which may be expected to provide the conditions for an increase in evolutionary variance through the exploitation of wider ecological niches (Collar *et al.*, 2010). By contrast, saxicolous habitat preferences could be expected to limit diversification rates by imposing constraints on morphological evolution and establishing a narrow adaptive peak for ecologically relevant traits (Hansen & Martins 1996; Collar *et al.* 2010). However, this does not seem to be the case here, as evolutionary rates did not differ between habitat types for any of the examined traits of either males or females (Table 2; but see below for SD). Whether this is a general trend

observed in the entire genus of wall lizards, or it is rather due to the low habitat variation observed in the Iberian and North African clade, would need to be further investigated.

### Habitat use and the evolution of sexual dimorphism

Separate examination of males and females reveals that habitat use has shaped phenotypic variation across lineages of Iberian and North African wall lizards (as is also the case in other lizard groups: e.g. Losos, 1990a,b; Vitt *et al.*, 1997; Melville & Swain, 2000; Collar *et al.*, 2010, 2011). But how does phenotypic evolution of males and females translate into macroevolutionary patterns of sexual dimorphism? Although some differences exist, general patterns of ecomorphological evolution are shared across the sexes in Iberian and North African wall lizards. Habitat effects are restricted to head morphology in both sexes. In both males and females, body size variation across lineages is best explained by a BM evolutionary model, not bearing signs of either directional or diversifying selection (Table 3). Instead, in both sexes, there is evidence of directional selection on trunk length, for which an OU model with a single adaptive peak exhibited the best fit to the data (Table 3). Male and female body size and shape evolve at the same pace (Fig. 4). Together, these results support the view that, despite the presence of marked sexual dimorphism, the members of both sexes are influenced in common ways by habitat variation and their phenotypes are driven by similar evolutionary processes. This may be in part the result of a largely shared pool of genes and genetic limitations to sexual differentiation (Lande, 1980) potentially leading to sexual conflict (Parsch & Ellegren, 2013).

Further, the evolution of some traits may be subject to anatomical constraints, which therefore link male and female patterns of variation to one another. For instance, the directional pattern of evolution observed for trunk length in members of both sexes, together with the slower evolutionary rate of this trait (Fig. 4; Table 4), suggest that this character is evolutionarily less labile compared to other body parts. Variation in trunk length is known to be associated with a modification of the number of vertebrae (Van Damme & Vanhooydonck, 2002; Bergmann & Irschick, 2012). Although body elongation has been repeatedly modified across the Squamata (Sites *et al.*, 2011), it is an evolutionary innovation that involves substantial embryonic reprogramming of a clock-and-wave mechanism controlling the production of somites (Gomez *et al.*, 2008), which may not be easily attained across closely related taxa. The slow evolution of vertebral number in lacertids, as compared to other squamate groups, may suggest that this trait is evolutionarily preserved in this family (Bergmann & Irschick, 2012), which translates into reduced evolutionary rates as

compared to other traits. Although sexual dimorphism in vertebral number is a derived feature of the Lacertidae (Arnold, 2004) and is known to occur in several *Podarcis* species (Arnold, 1973; Kaliontzopoulou *et al.*, 2008a), it appears then that both male and female vertebral evolution are constrained in this group of lizards.

Despite the global concordance between male and female phenotypic patterns, however, small differences between the sexes in evolutionary tempo and mode yield macroevolutionary SD patterns that vary remarkably across traits. This is particularly evident for head dimensions, where the balance between sex-specific responses critically influences macroevolutionary patterns of SD. On the one hand, our analyses indicate that head width evolved towards different optima in saxicolous and generalist lineages in both sexes, but this effect does not translate into variation in head width SD across habitats (Table 3). This means that, although diversifying selection is driving males and females of generalist lineages towards a higher phenotypic value for HW, as compared to saxicolous ones, this effect is similar enough in both sexes to preclude variation of SD across habitat types for this trait. Indeed, the estimated difference in phenotypic optima between saxicolous and generalist lineages was similar in males ( $\beta_{\text{sax}} - \beta_{\text{gen}} = -0.048$ ) and females ( $\beta_{\text{sax}} - \beta_{\text{gen}} = -0.041$ ; Table 2), suggesting that the amount of evolutionary divergence due to habitat use is similar across the sexes. By contrast, we found evidence for diversifying selection due to habitat in head height for males, but not for females (Table 3). This difference in evolutionary mode between the sexes translates into an evolutionary variation of head height SD across habitats, where generalist lizards are more dimorphic (Fig. 3). Sexual differences in head height are a common pattern in lizards (Braña, 1996; Herrel *et al.*, 1996, 2007; Olsson *et al.*, 2002; Kaliontzopoulou *et al.*, 2008b), and they are known to be driven by sexual selection on male bite force enhancing fighting capacity and dominance (Stamps, 1983; Huyghe *et al.*, 2005; Husak *et al.*, 2006; Lailvaux & Irschick, 2007). On the other hand, physical constraints imposed by a saxicolous lifestyle are expected to counteract the effect of sexual selection, limiting the potential of males for optimizing head shape in relation to bite force, as natural selection would drive both male and female phenotypes towards relatively flatter heads in these habitats (Vitt *et al.*, 1997; Stuart-Fox & Moussalli, 2007). This kind of interaction is observed at the intra-specific level in *Podarcis bocagei* (Kaliontzopoulou *et al.*, 2010a), and our results suggest that it also occurs at a higher evolutionary level for Iberian and North African wall lizards more generally.

However, interpreting the association between macroevolutionary patterns of SD and the underlying male and female mechanisms of phenotypic evolution is not always straightforward. In some cases, this is due to the fact that some of the statistical tools necessary for a full

assessment of biological patterns are not yet available. For instance, when using phenotypic models to investigate the evolution of hindlimb length we found that male, female and SD lineage values are best explained by a model of directional evolution (OU1: Table 3). This means that, although the best-fit evolutionary model is the same for both sexes in this case, the detailed evolutionary dynamics and corresponding model parameters probably differ, as OU1 is also given the highest support for HLL SD (Table 3), mirroring the hypothetical scenario of Fig. 1a2. Such a hypothesis would imply that either the distance between the ancestral and optimal trait value or the strength of selection differ between male and female phenotypes, leading to different evolutionary interpretations in each case. However, a statistical framework for comparing these model parameters across traits has not been yet developed. Recent advances in phylogenetic comparative methods already allow the comparison of evolutionary rates across traits (i.e. Adams, 2013) or variation in mode-related model parameters across time (i.e. Slater, 2013). A statistical framework that would allow the comparison of OU model parameters across different traits would therefore be a useful extension of these methods.

It is also important to remark that when using phylogenetic comparative tools to investigate the evolution of emergent species properties such as sexual dimorphism, it is important to always link inferences on the emergent trait to the underlying raw traits, in order to verify whether the inferred macroevolutionary mechanisms are biologically meaningful. For instance, the results obtained with respect to the evolution of body size and relative trunk length may seem sensible when male/female phenotypes and the degree of sexual dimorphism are examined in isolation. Joint examination, however, reveals that evolutionary inference may be flawed in this case. Indeed, we found that habitat use triggers a faster evolution of body size and size-corrected trunk length sexual dimorphism in generalist lineages (Table 3). However, examination of the evolution of male and female phenotypes reveals that this increase in evolutionary rates observed for the degree of sexual dimorphism is not attributable to a habitat-related shift in evolutionary variances or trait mean values of either of the sexes, as the best-fit models where a simple BM and a single-peak OU for body size and relative trunk length correspondingly (Table 3). From a biological point of view, such a result is evolutionary impossible, as the degree of sexual dimorphism cannot be modified without a corresponding modification of the underlying male and female phenotypes that comprise it. More generally, it seems biologically reasonable to predict that emergent species properties could never evolve under an evolutionary model more complex than that driving the evolution of the underlying raw traits. This is because the parameters of evolutionary models that aim

at describing the change of an emergent species property across a phylogeny (e.g. sexual dimorphism) need to be in concert with the evolutionary dynamics of the raw traits of interest (e.g. male and female phenotypes). Again, the development of methods for comparing and integrating model inference across traits would be a fruitful direction of theoretical development, which could aid us to understand how the balance of different evolutionary processes determine the macroevolutionary phenotypic patterns we observe in nature.

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## Supporting information

Additional Supporting Information may be found in the online version of this article:

**Table S1** Results of likelihood ratio tests between pairs of nested models fit on each phenotypic trait for females, males and the degree of SD.

**Table S2** Relative evolutionary rate (Relative  $\sigma^2 = \sigma_{\text{male}}^2 / \sigma_{\text{female}}^2$ ), likelihood for a two-rate ( $\log\text{Lik}_{2R}$ ) and a single-rate ( $\log\text{Lik}_{1R}$ ) model, likelihood ratio and corresponding *P*-value for comparisons of evolutionary rates across the sexes.

**Table S3** Relative evolutionary rate (Relative  $\sigma^2 = \sigma_{\text{trait1}}^2 / \sigma_{\text{trait2}}^2$ ), likelihood for a two-rate ( $\log\text{Lik}_{2R}$ ) and a single-rate ( $\log\text{Lik}_{1R}$ ) model, likelihood ratio and corresponding *p*-value for comparisons of evolutionary rates between pairs of traits.

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