



Context-dependent expression of sexual dimorphism in island populations of the common wall lizard (*Podarcis muralis*)

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Received 19 August 2014; revised 14 October 2014; accepted for publication 19 October 2014

The condition-dependent sexual dimorphism model explains the evolution and maintenance of sexual dimorphism in traits targeted by sexual selection, and predicts that the magnitude of sexual dimorphism depends on the variability of individual condition, male traits being more variable than female corresponding traits. Most convincing examples concern insects, while studies among vertebrates are scanty because manipulating condition often is not possible, and the time to reach sexual maturity may be too long. Islands offer a unique opportunity to compare how the environment affects the expression of sexual dimorphism, since they represent 'natural experimental sets' in which different populations of the same species may experience alternative environmental constraints. We investigated the occurrence of context-dependent expression in sexual dimorphism of head shape in insular populations of the common wall lizards (*Podarcis muralis*) inhabiting the Tuscan Archipelago (Tyrrhenian Sea). Alternative models were formulated: H_0 assumes that the sexual dimorphism is uninfluenced by islands, H_1 assumes the only effect of phylogeny, H_{2A} and H_{2B} account for the biogeography of the archipelago (island size and distance from the mainland), while H_3 assumes island-specific effects on sexual dimorphism. Models were compared using Akaike's information criterion adjusted for multivariate analyses. All hypotheses performed better than H_0 , but H_3 largely outperformed all other alternative hypotheses, indicating that environmental features of islands play an additive effect to ontogenetic, biogeographic and genetic factors in defining variation in head shape sexual dimorphism. Our results support the hypothesis of a context-dependent sexual dimorphism in common wall lizards. © 2015 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2015, 114, 552–565.

ADDITIONAL KEYWORDS: condition dependency – geometric morphometrics – islands – sexual selection.

INTRODUCTION

The 'condition-dependent sexual dimorphism hypothesis' (CDS, Bonduriansky, 2007) has been proposed to explain the evolution and maintenance of sexual dimorphism in traits targeted by sexual selection.

Classical theories of sexual selection state that the expression of secondary sexual traits entails large energetic costs of production and maintenance (Zahavi, 1975; Hamilton & Zuk, 1982; Rowe & Houle, 1996). Hence, sexual traits should reliably signal male attributes since only individuals of high genetic quality can meet the costs associated with exaggerated and costly secondary sexual traits (Zahavi, 1975; Andersson, 1982). Honest signalling is therefore

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maintained by the co-evolution of trait expression and condition dependency (Cotton, Fowler & Pomiankowski, 2004a), since condition is the result of the interaction of several metabolic pathways, which are in turn depending on multiple loci, and sexual selection is expected to capture some of this genetic variation due to its genetic correlation with condition (Rowe & Houle, 1996).

The CDS model assumes that individual condition depends on both the availability of resources in the environment and the genes affecting the efficiency in extracting and converting them into metabolic resources. In turn, the condition affects the relative rates of resource allocation to sexually selected traits, but with different underlying mechanisms in the two sexes: trait expression is controlled by sexual selection in males, promoting an improvement of attractiveness and strength, and by natural selection in females, acting directly on survival. Differential allocation is also controlled by sex-linked genes, and the sex-dependent resource allocation regulates how relative allocation to each sex changes with increasing condition. Sexual dimorphism is therefore the result of the interaction between sex-linked genes and condition-dependent expression (see fig. 6 in Bonduriansky, 2007 for a general scheme of the model). Although all traits may be virtually affected by condition dependency, greater sensitivity to condition is expected to evolve in sexually selected traits, leading to the development of CDS, where variation in trait expression among males reflects phenotypic variation across levels of metabolic resource availability (Bonduriansky, 2007). Two main predictions follow CDS: firstly, sexual dimorphism (SD) varies according to the variability of individual condition, and secondly, male traits should be more variable than female corresponding ones. Both these predictions have been experimentally checked and several examples have been reported in different traits and species, particularly in insects (Bonduriansky & Rowe, 2005; Bonduriansky, 2007; Kemp, 2008; Cothran & Jeyasingh, 2010; Okada & Miyatake, 2010). For example, males of different species of Diptera grown in poor conditions develop female-like phenotypes, contrary to what they do when grown in rich environments (Cotton, Fowler & Pomiankowski, 2004b; Bonduriansky & Rowe, 2005; Bonduriansky, 2007).

'Condition' usually refers to the total amount of resources acquired by an individual that can then be allocated to fitness-relevant traits (Rowe & Houle, 1996; Wolf, Harris & Royle, 2008). However, individual condition is not independent of the 'context', i.e. the environment where individuals live, which can severely affect the condition dependency of sexual traits (Wolf *et al.*, 2008; Cothran & Jeyasingh, 2010).

For instance, high intensity of environmental stressors (e.g., extreme temperature, lowering in food availability and quality, high competition and predation risk, etc.) may emphasize the differences among males in the ability to compete under limiting factors, therefore in their condition and, consequently, in the amount of resources finally available for the expression of sexually selected traits (Wolf *et al.*, 2008; Cothran & Jeyasingh, 2010). By contrast, in habitats where environmental stress is low, less variation in sexually selected traits is expected (David *et al.*, 2000; Cotton *et al.*, 2004b; Cothran & Jeyasingh, 2010). As a result, the intensity of SD should depend not only on the genotype but also on the environmental contexts in which organisms live. Secondary sexual characters through condition dependence are expected to show a context-dependent expression determined by resources availability and opportunities for their exploitation (Wolf *et al.*, 2008; Cothran & Jeyasingh, 2010). If the environmental stress changes, SD is expected to vary accordingly, and the degree of context-dependence in secondary sexual traits should also be greater than in other non-sexually selected traits, including the homologous traits in females (Bonduriansky, 2007).

Examples of CDS are scarce among vertebrates, and most studies only report correlations between the variability of some environmental factors and the expression of SD (e.g., Post *et al.*, 1999; Weladji *et al.*, 2005). However, experimental manipulations of condition are needed to demonstrate context- or condition-dependent effects on SD. Unfortunately, complications with vertebrates arise because manipulating conditions are hard to achieve in controlled experiments. A good compromise is offered by the so-called 'natural experiments' (like islands, high mountains, lakes, etc.), in which several populations of the same species may have independently adapted under different environmental regimes, thus experiencing different levels of environmental stress. Islands are case in point since isolation can produce different level of stress by increasing intra-specific and/or inter-specific competition, predation risk, inability for dispersal, or limiting the availability of resources and optimal habitats (Crnobrnja-Isailovic, Aleksic & Bejakovic, 2005). Thus, focusing on island populations, and comparing the intensity of SD among them offers a real opportunity to investigate the effect of the environment on the expression of SD in vertebrates.

We address these topics using different populations of the common wall lizard (*Podarcis muralis* Laurenti, 1768), a small lizard (snout-vent length, SVL, 45–75 mm) inhabiting the islands of the Tuscan Archipelago (Tyrrhenian Sea, Central Italy). The species is widespread in Southern and Central

Europe (Sillero *et al.*, 2014) and mates multiply and produces on average two clutches per year (Sacchi *et al.*, 2012). SD is appreciable, males being longer and with larger head than females (Biaggini *et al.*, 2011). Despite natural selection may contribute to the development of SD when sexes differ in ecological traits, such as habitat or prey exploitation (Slatkin, 1984) or when sexes differ in reproductive investments (e.g., fecundity selection, Shine, 2000; Colleoni *et al.*, 2014), sexual selection plays a relevant role in shaping SD, particularly when male–male competition is intense (e.g., Kaliontzopoulou *et al.*, 2008). As in other lizards, male common wall lizards compete over females and there is a selective pressure for increased male body size and enlargement of combat-related traits, mainly the head size (Sacchi *et al.*, 2009). Larger-headed males bite harder, and head shape has been show to be an excellent predictor of bite performance (Herrel *et al.*, 2001). Thus, head shape can be reliably considered a stronger determinant of male mating success in intra-sexual competition.

The Tuscan Archipelago (Fig. 1) embraces a group of seven major islands, the largest of which is the Elba Island, and some minor islets and rocks located between Tuscany and Corsica. Islands widely differ in their ecological features and geological formation, and common wall lizards occur in seven islands and islets (Table 1). Recent molecular analyses supported the occurrence of two main genetic lineages in the archipelago: the *P. m. colosii* clade inhabiting Elba, Pianosa, Palmaiola and La Scola, and the *P. m. brueggemanni* clade occurring in all the other islands and islets (Bellati *et al.*, 2011).

In this paper, we assessed if the variability of environmental features of islands could represent a stress factor affecting the expression of SD in this species, according to the prediction of CDS model. In detail, we specifically assessed if (i) head shape has some degree of context-dependent expression in this species; (ii) SD intensity varies among insular populations; and (iii) variation in head shape among islands is more pronounced in males than in females, as specifically predicted by the CDS model.

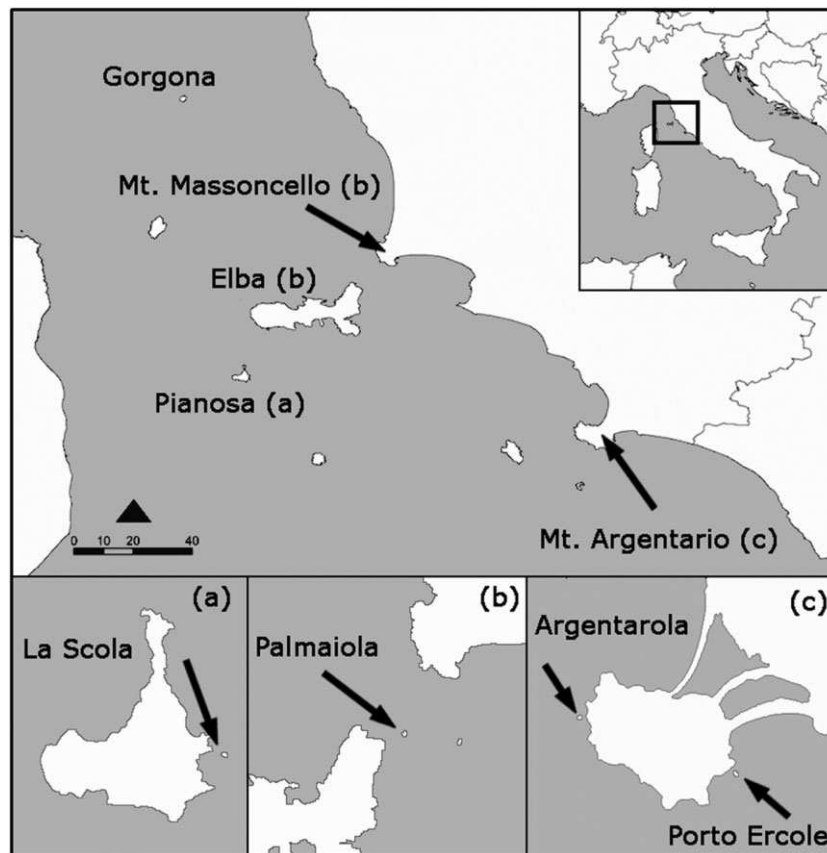


Figure 1. Islands and paleo-islands of the Tuscan Archipelago inhabited by common wall lizards.

Table 1. Features of the seven islands and two paleo-islands in the Tuscan Archipelago (Central Italy) inhabited by common wall lizards

Island/islet	Coordinates (UTM)	Size (km ²)	Distance from mainland (km)
Gorgona	572732E, 4808452N	2	37
Elba	605649E, 4737006N	224	10.4
Palmaiola	620520E, 4746970N	0.08	7.5
Mount Massoncello	623080E, 4757162N	34.9	0
Pianosa	588408E, 4714838N	10.3	51.2
La Scola	590782E, 4715190N	0.02	50
Mount Argentario	677109E, 4696839N	60.3	0
Argentarola	671267E, 4698337N	0.012	0.45
Porto Ercole	682035E, 4694461N	0.063	0.35

Table 2. Samples of males and females used to estimate sexual dimorphism of head shape in every island. Vouchers refer to the specimens' code numbers in the catalogue of La Specola' Natural History Museum (Firenze, Italy)

Island	Females	Males	Vouchers
Mount Argentario	7	7	18837, 18838, 18839, 9645, 9644, 9655, 9642, 9649, 9652, 9638, 9653, 9650, 9651, 9639
Argentarola Islet	16	13	34702, 31609, 31608, 31610, 31607, 30165, 30166, 30167, 22899, 22895, 22897, 22905, 22893, 22901, 22906, 22909, 22904, 22908, 22907, 22900, 22896, 22892, 22898, 22894, 22902, 31608, 31609, 31610, 31607
Elba Island	15	29	34557, 34558, 9632, 9636, 9702, 9640, 9634, 9637, 9633, 9627, 9619, 9621, 9620, 9630, 9623, 9622, 9625, 9629, 9703, 9631, 9616, 9617, 9618, 9624, 9626, 9628, 18722, 18723, 18724, 4613, 4612, 4618, 4615, 4616, 4611, 4614, 30258, 30265, 30266, 30268, 30267, 30259, 30264, 30263
Gorgona Island	10	10	36083, 36084, 33575, 33576, 33580, 33579, 33577, 33581, 33578, 25444, 25461, 25445, 25468, 25446, 25451, 25464, 25448, 25455, 25470, 25469
La Scola Islet	6	15	36881, 36882, 36883, 36884, 36885, 36886, 36887, 10918, 10924, 10921, 10922, 10917, 10927, 10920, 10919, 10926, 10925, 10923, 10916, 34555, 34556
Palmaiola Islet	9	13	10257, 10258, 10259, 10260, 10261, 10262, 10263, 10264, 10265, 10266, 10267, 10268, 10269, 10270, 10271, 10272, 30630, 30631, 30632, 30633, 30634, 30635
Pianosa Island	12	13	30122, 30126, 30125, 30123, 30128, 30124, 30121, 30120, 30129, 30127, 30119, 37119, 37118, 37120, 37121, 37123, 37124, 37122, 37125, 37114, 37116, 37113, 37112, 37115, 37117
Mount Massoncello	5	10	35139, 35140, 35141, 35142, 35138, 20588, 20589, 20590, 8158, 8157, 2884, 34407, 18789, 18790, 18791
Porto Ercole Islet	4	15	28950, 28951, 28952, 22490, 22486, 22487, 22489, 22485, 22488, 9608, 9613, 9614, 9606, 9609, 9605, 9612, 9610, 9607, 9611
Total	84	125	

MATERIAL AND METHODS

SAMPLES AND LANDMARKS

We examined a total of 209 specimens (125 males and 84 females, Table 2) from all the seven insular populations of the Tuscan Archipelago, as well as specimens from the two paleo-islands of Mount Argentario and Mount Massoncello (Lanza, 1984, Fig. 1). These mounts had been isolated until the last glaciation,

and were included to increase sample size. All the specimens are preserved in the 'La Specola' Zoological Museum (Florence, Italy, Table 2). Head images were obtained using a Nikon D50 camera at a 1.2 million pixel resolution, equipped with a Nikkor 60 mm AF-S Micro lens, at a fixed distance of 18 cm. Head shape was analysed using geometric morphometrics (Bookstein, 1997; Dryden & Mardia, 1998), which bases on landmark configurations to decomposes the

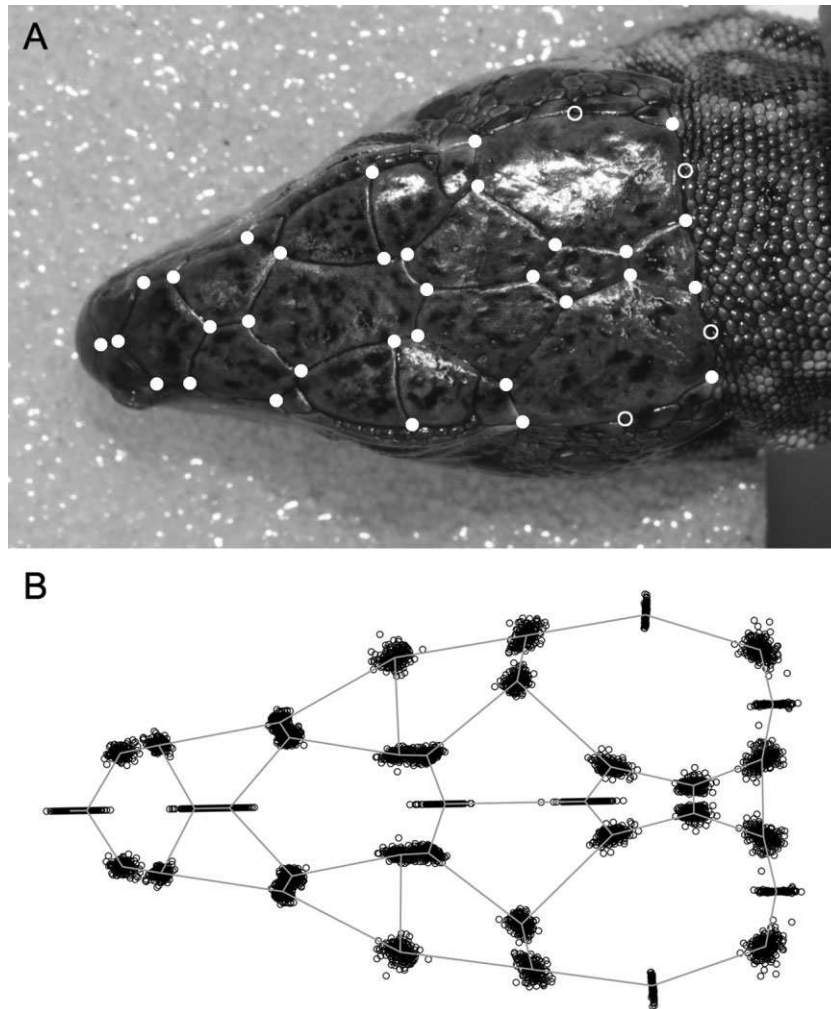


Figure 2. Location of landmarks (filled circles) and semi-landmarks (open circles) used to analyse head shape of common wall lizards (A), and consensus configuration of landmarks after mirroring and superimposition (B).

shape of an object into components of size and pure shape. Size, termed centroid size (CS), is defined as the square root of the sum of the squared distances between each landmark and the specimen centroid. Two-dimensional coordinates of 32 landmarks and four semi-landmarks (Fig. 2A) were digitized for each specimen using TpsDig2 (Rohlf, 2010; available at: <http://life.bio.sunysb.edu/morph/>), and specimens were scaled to unit centroid size and superimposed by a generalized procrustes analyses (GPA). For each specimen, we computed a new perfectly symmetric landmark's configuration following Klingenberg, Barluenga & Meyer (2002): first, a reflected copy of each configuration was generated; second, the original and mirrored configurations of a sample combined were superimposed; third, the coordinates of corresponding landmarks in original and mirrored configuration of each specimens were averaged leading to a perfectly symmetric configuration (Fig. 2B). A princi-

pal components analyses (PCA) was carried on the variance-covariance matrix of the landmark coordinates, and the set of PCs scores was used as shape variables. Since both semi-landmarks and mirroring process reduce the dimensionality of the data with respect to the theoretic number of $(2 \times p) - 4$ dimensions (i.e., $(2 \times 36) - 4 = 68$), where p is the number of landmarks (Dryden & Mardia, 1998), we estimated the dimensionality of data by counting the not zero eigenvalues of the variance-covariance matrix of the landmark configuration. We found 34 not zero eigenvalues, so we used the first 34 PC scores as head shape variable set in the multivariate analyses.

ANALYSIS OF SD'S PATTERNS AMONG ISLANDS

To look for island-specific effects on morphological differences in head shapes of males and females, we

needed to control for general patterns affecting sexual size dimorphism, such as ontogenetic, phylogenetic and biogeographic patterns, not directly related to the context-dependent expression of SD. To do this, we combined multivariate analyses of shape of geometric morphometrics, and information-theoretic model comparison (ITMC; Stephens *et al.*, 2005). ITMC is a general well known approach in ecology (Johnson & Omland, 2004), used to compare different *a priori* hypotheses, each represented by a model, and search for the best one (Anderson, Burnham & Thompson, 2000; McIntire & Fajardo, 2009). Since the competing models are ranked on the basis of an information criterion, which measures the amount of information not captured by the model, weighed for the complexity of the model itself (Anderson *et al.*, 2000), we formulated alternative MANOVA models, each representing alternative hypotheses explaining the observed shape patterns. In formulating the competing hypotheses, the null hypothesis H_0 assumed that variability of head shape SD among populations was wholly explained by the ontogenetic pattern, and predicted that SD increases with increasing size of individuals. The alternative hypotheses (H_1 , H_2 , H_3 , see next section for a detailed description of all the alternative hypotheses we tested) included the effects of ontogeny and those of additional factors potentially affecting shape variation between sexes (i.e., phylogeny, biogeography and island-specific effects). The ITMC ranks hypotheses indicating which of them works better and, consequently, what is the relative importance of each explaining variable other than ontogeny in explaining the observed extent of SD in head shape.

FORMULATION OF HYPOTHESES

We formulated four competing hypotheses:

H_0 The *null hypothesis*: head shape of males and females depends only on the ontogenetic pattern. The MANOVA model was generated using sex, body size (logarithm of SVL) and their interaction as predictors ($\text{Sex} \times \text{SVL}$).

H_1 The *phylogenetic hypothesis*: head shape of males and females is moulded by ontogenetic and phylogenetic processes, so different expressions of SD are expected for different genetic lineages. Phylogenetic effects were estimated through a two levels factor, one level for *P. m. colosii* (i.e., populations inhabiting Palmaiola, Elba, Pianosa islands and La Scola Islet) and one level for *P. m. brueggemanni* (i.e., populations from the paleo-islands of Mount Massoncello and Mount Argentario, the Argentarola Islet and the Porto Ercole Islet). The corresponding MANOVA model was generated by adding H_0 with a two levels factor accounting for clades ($\text{Sex} \times \text{SVL} \times \text{clade}$).

H_2 The *biogeographic hypothesis*: head shape of males and females results from the biogeographic patterns of the islands other than the simple effect of ontogeny (MacArthur & Wilson, 1967). According to their size, islands were classified

as 'small' (La Scola, Palmaiola, Argentarola and Porto Ercole, mean size = 0.027 km²) and 'large' (Massoncello and Argentario mounts, Elba, Gorgona, and Pianosa, mean size = 69 km²), whereas according to the distance from the mainland they were classified 'as mainland' (Massoncello and Argentario mounts), 'continental' (Elba, Argentarola, Porto Ercole and Palmaiola, mean distance = 4.6 km) and 'oceanic' islands (Pianosa, La Scola and Gorgona, mean distance = 45 km). The biogeographic hypothesis was thus represented by two different MANOVA models generated by adding H_0 with the main effect of size (H_{2A} : $\text{Sex} \times \text{SVL} \times \text{size}$) or distance (H_{2B} : $\text{Sex} \times \text{SVL} \times \text{distance}$).

H_3 The *context-dependent hypothesis*: head shape of males and females, besides the effects of ontogeny, is moulded by island's environmental conditions. For each island we measured a set of 15 variables capturing topography, climate, land use and human disturbance (Supporting Information, Table S1). Since all these variables may be affected by island biogeography as well as by phylogeny, we used a Redundancy Analysis (RDA; Legendre & Legendre, 1998) to assess the amount of variance in habitat variables independent of size, distance from the mainland and clade (*colosii* vs. *brueggemanni*) of islands, and to obtain a single synthetic variable that explained as much as possible that variance. The numerical output of RDA (Supporting Information, Table S2) showed that the first canonical axis explained 30.7% of the total variance of data ($F_{1,5} = 2.617$, $P = 0.0495$, permutations = 9999) and 74% of the constrained variance, suggesting that major trends have been modelled. On the other hand, the first principal component explained 22.5% of the total variance of data and captured 38.4% of the unconstrained one. This PC clearly separated islands according to environmental variables (Fig. 3), and was then used as synthetic variable to characterize the habitat features not affected by biogeographic or phylogenetic patterns. The model to evaluate the effect of islands' environmental conditions on lizard SD was therefore obtained by adding the first PC scores to H_0 ($\text{Sex} \times \text{SVL} \times \text{Hab}$).

The comparison among models was carried out by means of the Akaike's Information Criterion (AIC), adjusted for multivariate models (Hurvick & Tsai, 1989). Since data come from island populations, individuals result clustered (i.e., data are not fully independent) leading to a possible overestimation of significance tests and AIC differences. Generally, the analysis of this kind of clustered data requires the use of mixed models, including island identity as random effect, but multivariate analyses allowing the inclusion of random effect are not available. However, the scores obtained through the PCA on the aligned coordinates are independent, and can be analysed using linear mixed model. Despite the fact that this approach misses the multivariate structure of data, it allows some evaluation of the extent of random effects on head shape. Thus, we run a linear mixed model for the first five PCs (one model for each one) including the same fixed structure as in MANOVAs, and a random effect for the islands. The analyses were

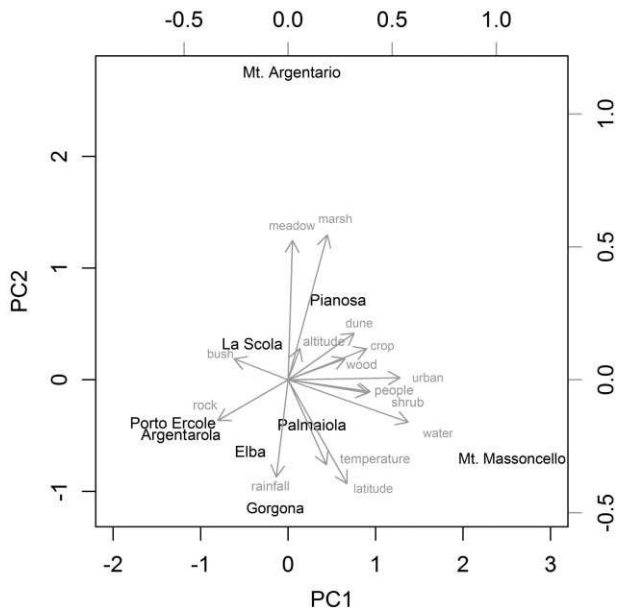


Figure 3. Ordination plot of islands and paleo-islands on to the first two PCs summarizing the unconstrained variance of the Redundancy Analysis performed on 15 environmental variables (see Supplementary Material for details) constrained by size, distance of the island from the mainland and genetic clade of insular populations.

performed only for the best model resulting from model comparison. The results confirmed that the three-way interaction significantly affected the head shape (see Supporting Information), suggesting that data clustering within islands did not seriously affect our models.

In order to assess the size effect of the predictors within each alternative model, we applied a variation partitioning analysis (Borcard, Gillet & Legendre, 2011), which uses the coefficients of determination in order to partition the variation of the dependent variables among alternative sets of explanatory variables, thus allowing the estimation of the amount of variation univocally associated to a single predictor rather than to a combination of them. We firstly estimated the pure effects of the phylogenetic, biogeographic, and condition-dependent effects additive to the ontogenetic model, by comparing H_0 with each of the alternative hypotheses H_1 , H_{2A} , H_{2B} , and H_3 in four independent analyses. In a second step, we partitioned variation among the hypotheses alternative to H_0 in order to disentangle the pure effect of the islands in the condition-dependent model, while controlling for the overlapping effects of ontogeny, phylogeny, and biogeography. We therefore performed three independent analyses, one comparing H_1 , H_{2A} , and H_{2B} , one for H_3 , H_1 , H_{2A} , and one for H_3 , H_1 , and H_{2B} , respectively.

Finally, we used multivariate homogeneity of groups dispersions (Anderson, 2006), which is a multivariate analogue of Levene's test for homogeneity of variances, to test if shape variability among islands was larger in males than in females. Multivariate dispersion for each sex was estimated by the average procrustes distance to the group centroid, and a permutational ANOVA ($N = 999$, stratified within island) was used to test if males were more variable than females.

RESULTS

Irrespective of the islands, head size increased with body size ($F_{1,205} = 691.1$, $P < 0.0001$), males had larger heads than females ($F_{1,205} = 966.7$, $P < 0.0001$), and sexual size dimorphism rose significantly with body size (sex \times SVL interaction: $F_{1,205} = 19.68$, $P < 0.0001$, Fig. 4A). Accordingly, all predictors in the ontogenetic model (H_0) were highly significant, suggesting that head shape changed with body size (Pillai's Trace = 12.06, d.f. = 1, $P < 0.0001$), was sexually dimorphic (Pillai's Trace = 17.21, d.f. = 1, $P < 0.0001$), and shape SD increased with increasing body size (Pillai's Trace = 1.509, d.f. = 1, $P = 0.047$, Fig. 4B). Indeed, small males and small females had near identical head shapes, but larger males showed wider and longer parietal scales and more pointed snouts than larger females (Fig. 4C, D).

In all the models alternative to H_0 there was at least one significant interaction of sex or SVL with the additional factor (Table 3), suggesting that the ontogenetic change was not enough to explain the whole variability of SD in head shape among insular populations. The model ranking using the Akaike's criterion (Table 3) completely supported the results of MANOVAs as the null hypothesis obtained the worst score, while all alternative models performed much better than it. Overall, the best model corresponded to context-dependent hypothesis (H_3), which showed the lowest AIC and an Akaike's weight > 0.999 . The full ranking of model was $H_3 > H_{2A} > H_1 > H_{2B} > H_0$. The ΔAIC with respect to the second best model was 19, supporting the occurrence of an effect of the habitat features of islands additive to the pure effects of phylogeny and biogeography.

In the best model, the effect of the three-way interaction Sex \times SVL \times Hab was highly significant (Table 3), supporting the hypothesis that the SD intensity varies according to the environmental features lizards experience in each island. Therefore, the different environmental conditions occurring in each island should promote different ontogenetic trajectories causing SD to be different from island to island. Additionally, the SVL \times Hab interaction was much more significant than the Sex \times Hab one, suggesting

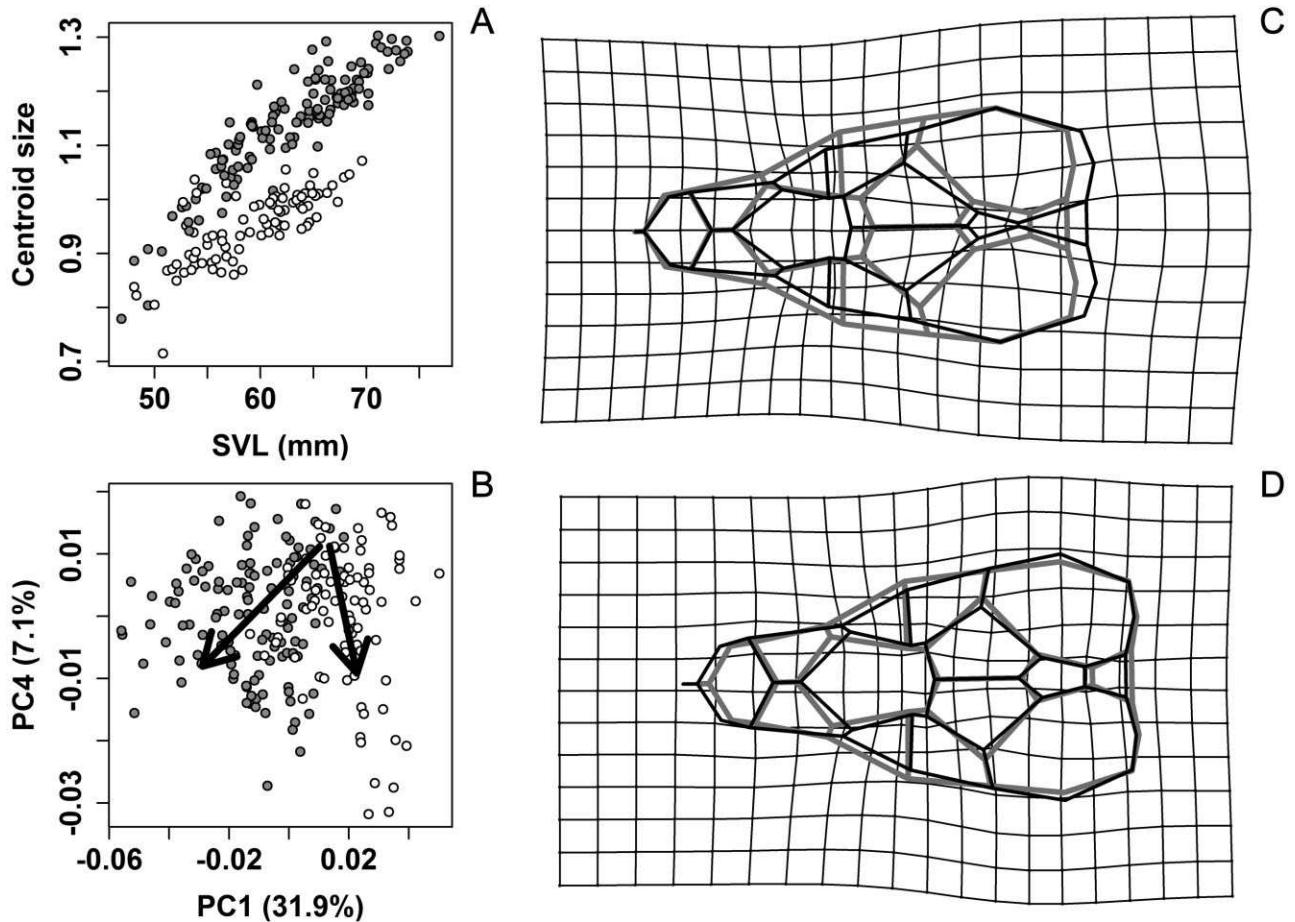


Figure 4. Variation of head size and head shape according to body size (SVL). (A) Allometric scaling of head size (estimated by the centroid size) in males (solid circles) and females (open circles). (B) Allometric scaling of head shape according to the first and fourth principal components on the landmark coordinates after GPA superimposition; symbols as in (A); black arrows represent the phenotypic change vectors of males and females from the smallest to the largest individuals. (C) Deformation grid of male head shape from the smallest (grey) to the largest (black) individual. (D) as in (C) for females.

that the environment acts more intensively on the allometric growth rather than on the gender difference itself.

The variation partitioning analysis comparing the null hypothesis with each of the alternative ones actually confirmed that H_1 , H_{2A} , H_{2B} , and H_3 have a relevant additive effect to that of the ontogenetic pattern associated with H_0 . Indeed, ontogeny alone explained 29.3% of head shape variation, whereas the specific contributions of the phylogeny, island size, and distance from the mainland were 6.2%, 10.6%, and 7.1% respectively (Fig. 5), and that of context-dependent model (H_3) was 9.9%. The same analysis used to compare the hypotheses alternative to H_0 with each other showed that: (i) the ontogeny (the common intersection among all models) was the major determinant of head shape variation, since it accounted for more than 25% of explained variance; (ii) biogeographic

and phylogenetic hypotheses were not additive, since from 3.1–6.4% of the whole variation of head shape was not shared between models, but was exclusively assigned to each of them (Fig. 6A); (iii) the context-dependent hypothesis (H_3) also has a pure effect independent from both phylogeny and biogeography, which varies between 2.0 and 5.5% representing the amount of head shape variation due to the specific features of each island (Fig. 6B, C); (iv) 4.2–5.6% of the head shape variation was assigned to the pure effect of phylogeny, accounting for the head shape variation proper to the *colosii* clade; and (v) 3.3–6.8% of the explained variation included within the context-dependent model but not by the phylogenetic one, and represents the biogeographic effect on the head shape variation due to the environmental features of islands (Fig. 6B, C).

Table 3. Model comparison and MANOVA tests; only interaction including sex and SVL are showed; K and w_i represent the number of parameters and the value of Akaike weight respectively

Hypothesis / Model		K	d.f.	Pillai's trace	P	Δ AIC	w_i
H ₃ : Context dependent	Sex × SVL × Hab	8	1	0.291	0.0018	0	> 0.999
	Sex × Hab		1	0.228	0.062		
	Sex × SVL		1	0.245	0.028		
	SVL × Hab		1	0.313	< 0.001		
H _{2A} : Biogeography A	Sex × SVL × Size	8	1	0.225	0.069	19	< 0.001
	Sex × Size		1	0.197	0.21		
	Sex × SVL		1	0.307	< 0.001		
	SVL × Size		1	0.405	< 0.001		
H ₁ : Phylogeny	Sex × SVL × Clade	8	1	0.240	0.035	27	< 0.001
	Sex × Clade		1	0.249	0.023		
	Sex × SVL		1	0.216	0.10		
	SVL × Clade		1	0.424	< 0.001		
H _{2B} : Biogeography B	Sex × SVL × Distance	12	2	0.293	0.82	97	< 0.001
	Sex × Distance		2	0.381	0.23		
	Sex × SVL		1	0.210	0.16		
	SVL × Distance		2	0.709	< 0.001		
H ₀ : Null hypothesis	Sex × SVL	4	1	0.230	0.047	147	< 0.001

The landmark configurations predicted by the H₃ model for the largest male and female for each island (Fig. 7) clearly showed that SD sensibly varies between islands, gradually increasing according to increasing PCA scores, and differences among islands concerned the intensity of the displacement between the sexes rather than the type or direction of the change. Moreover, marked differences occurred also among closer islands (e.g., Mount Argentario, Argentarola and Porto Ercole islets), confirming that difference in SD may be independent of geographic locations of islands.

Finally, in seven out of nine islands head shape was more variable in males than females (Fig. 8), and we can conclude consequently that the head shape variance among islands should be significantly larger in males than in females (0.0345 vs. 0.0317, multivariate homogeneity of groups dispersion test: $F = 4.831$, $P = 0.015$).

DISCUSSION

Theoretical models (Rowe & Houle, 1996) state that secondary sexual characters possess a condition-dependent expression, tending to be less expressed when individuals, above all males, are subjected to unfavourable conditions, leading to a condition-dependence expression of SD (Bonduriansky, 2007). Among the others, the main predictions of the CSD model are the variation of the intensity of SD in response to the variability of male condition, and a

wider variability in male traits rather than in the corresponding female ones. Moreover, both theoretical and empirical researches have been increasingly focusing also on the effect of the context in which individuals develop, which can deeply affect secondary sexual traits expression (Wolf *et al.*, 2008; Cothran & Jeyasingh, 2010).

Our analysis on the head shape variability among insular populations of common wall lizards revealed that this morphological trait is a markedly plastic trait, which can sensibly vary from island to island, even among the closest ones (Fig. 7). Consequently, head shape SD markedly differs among populations, being slightly appreciable in some cases (e.g., Porto Ercole) or markedly pronounced in some others (e.g., Elba and Mount Massoncello). Islands represent alternative environmental contexts (i.e., they differ in topography, climate, vegetation and human made alteration), which can determine different regimes of environmental stress. Specifically, this variation may sensibly affect the density of insular populations, males living in different islands endure weaker or harsher levels of intra-sexual competition depending on the specific features occurring locally, thus extremely affecting the resource allocation to the expression of sexually selected traits, and ultimately the SD intensity. According to the CSD hypothesis, we found that difference in head shape between males and females in all the nine islands substantially concerns the shape and extent of the parietal scales, and the difference in SD among islands pertains the

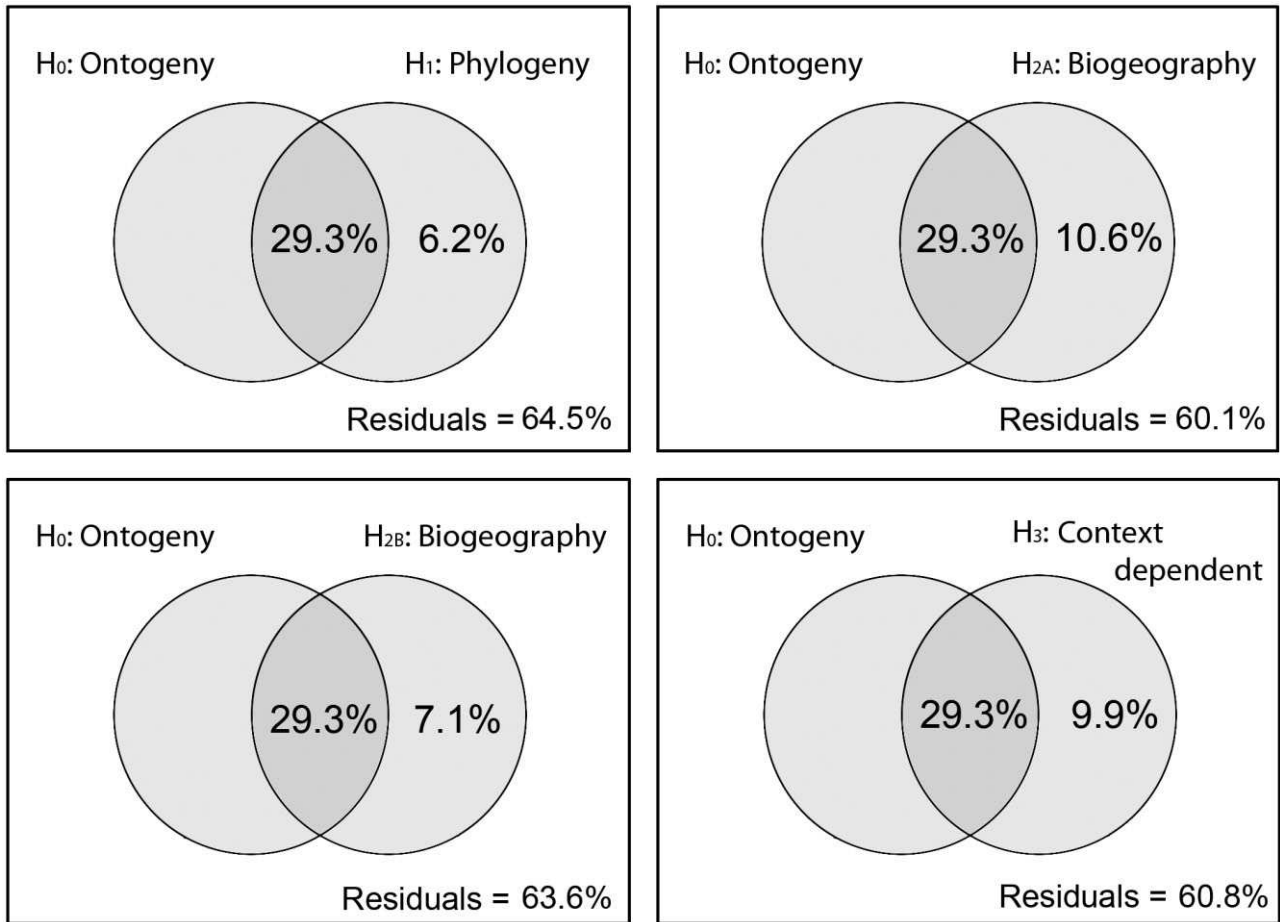


Figure 5. Variation partitioning diagrams for all hypotheses with respect to the ontogenetic one (H₀). Circles represent variation explained by each hypothesis, while numbers correspond to the percentage of variation associated to each circle. Due to the nesting procedure used to generate models (see methods) the value associated to intersecting areas (29.3%) has to be interpreted as the amount of variation due to the ontogeny also captured by the alternative hypotheses. The other values represent the pure variation associated to the hypothesis alternative to the null one.

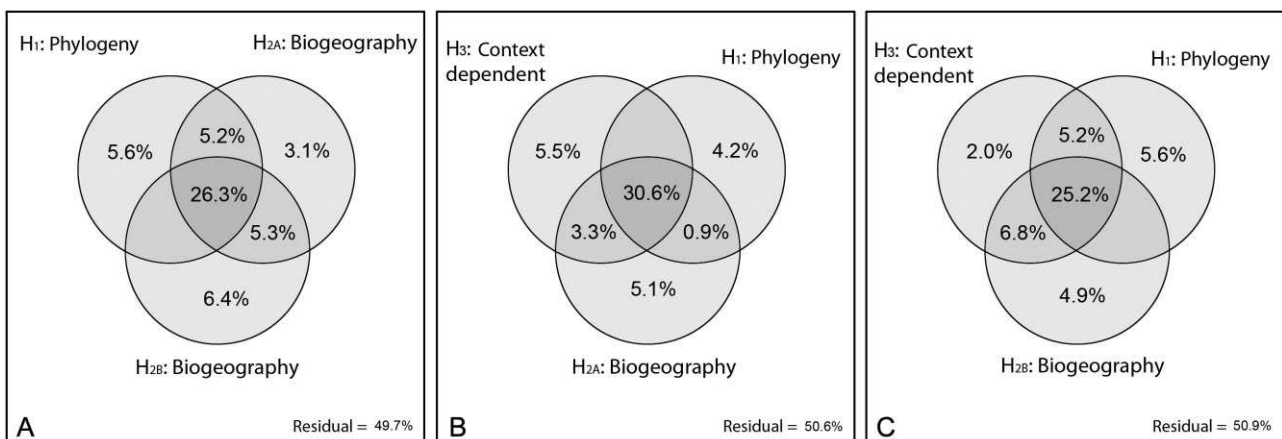


Figure 6. Variation partitioning diagrams among hypotheses alternative to H₀: phylogenetic hypothesis with respect to biogeographic ones (A) and condition-dependent hypothesis with respect to the phylogenetic and biogeographic ones (B, C).

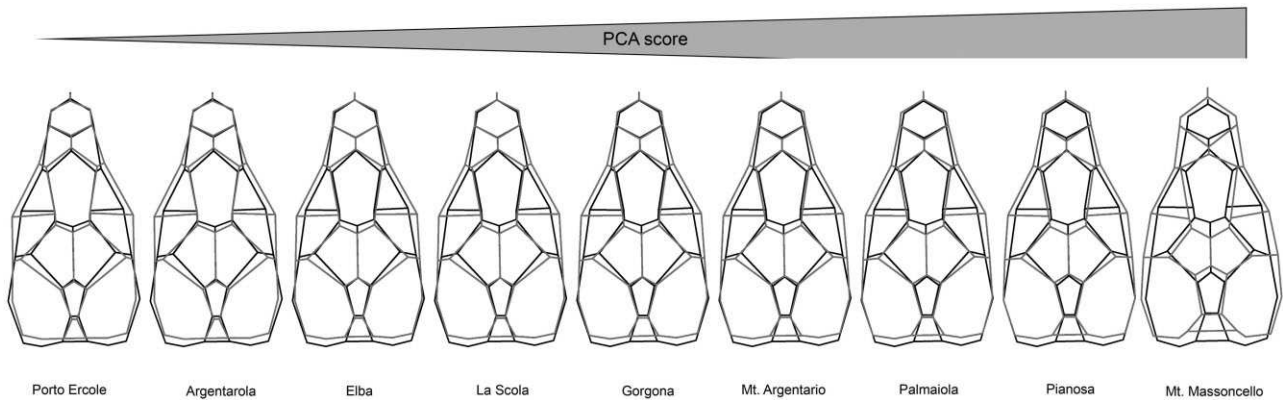


Figure 7. Mean landmark configuration for males (black) and females (grey) predicted for every islands by the condition-dependent model (H_3) according to increasing PCA score with male and female body sizes settled to their mean values.

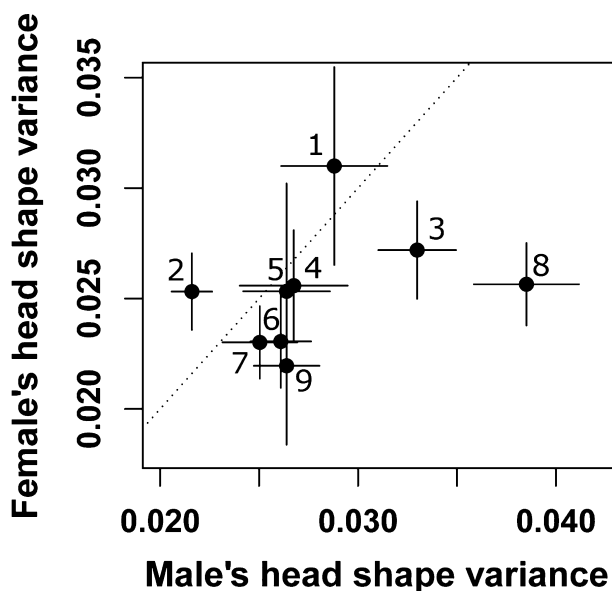


Figure 8. Mean head shape variance of male and female common wall lizards in each islands. Dotted line represents equal variances for the two sexes; points below the line have variances larger in males than in females, while the opposite occurs in points above the line.

magnitude of this divergence, but not its pattern. In other words, males and females follow the same pattern of shape divergence, but the process apparently works at different rates or, alternatively, ends at different times in each insular population. We interpret this pattern as a direct effect of environmental stressors (i.e., the context) on the ability of males to exploit resources in the environment and allocate them firstly to the condition, and then to the head shape differentiation.

Actually, other factors than condition-dependent expression can deeply affect the SD of head shape in

lizards, first of all ontogenetic changes (Bruner & Costantini, 2007; Kaliontzopoulou *et al.*, 2008), but also genetic differences among insular populations (Bellati *et al.*, 2011), as well as adaptive or ecological processes working at insular scale, such as phylogenetic (i.e., evolutionary), and biogeographic patterns. For instance, according to Bergmann's and Allen's rules, body shape (such as body size vs. extremity length) changes with latitudes and cold/warm climates (Fukase *et al.*, 2012), even if Bergmann's rule is highly controversial in ectotherms (e.g., Ashton & Feldmann, 2003). Moreover, the morphological variation between mainland and insular populations of *Liolaemus pictus* in Southern Chile has been related to the prolonged reciprocal isolation experienced by these populations during the last maximum glacial period, when geomorphologic and bioclimatic features of this area were largely modified leading to the formation of the present archipelago (Vidal *et al.*, 2006). Furthermore, in two cogenetic species of the one studied, *P. bocagei* and *P. hispanica*, fluctuating asymmetry in head shape was higher on remote islands than on those located close to the mainland (Băncilă *et al.*, 2010).

In this paper we were able to disentangle the confounding effects of ontogenetic, phylogenetic, and biogeographic processes from the pure effects of islands, and we estimated the effects size of the islands to be around 2.0–5.5% of the whole head shape variability. In other words, till up 5.5% of the variability in head shape depends exclusively on the island features (i.e., their geology, vegetation, animal community, ecological interactions between species), and therefore should not be considered dependent on the populations history (i.e., the colonisation pattern and the time at which the species colonised the islands), nor on the islands size and position with respect to the mainland. Furthermore, pure island effect was

appreciable, since it was similar in proportion to the one assessed for phylogeny (4.2–5.6%), and biogeography (3.1–6.4%). Variation in predator abundance and competitors on islands, microclimatic differences, as well as differences in food resources quality and availability have been actually invoked to explain divergence in morphology, diet and genetic variability in island populations (Irschick *et al.*, 1997; Clegg & Owens, 2002; Calsbeek & Smith, 2003). Thus, our results support the hypothesis that a significant portion of head shape variability linked to SD may depend on the island context, and consequently differences in SD expression among insular populations may be related to difference in the ecological features among the investigated islands.

The CDS model also predicts that traits representing the main target of intra-sexual selection could show a greater displacement from the female phenotype, which is controlled by natural selection for viability (Bonduriansky, 2007). The displacement is a measure of viability costs paid by males to increase their success in sexual competition, and corresponds to the condition dependence of trait expression (Bonduriansky, 2007). Thus, SD should change because male phenotype diverges from the female phenotype, and our study provides support for this. Indeed, we showed that head shape SD resulted by a prolonged divergence of males from females and, consequently, the variation in head shape SD among islands resulted from a different extent in that divergence.

Another important result of this study supporting the occurrence of CDS in head shape of the studied species was the higher inter-islands variability in males compared to females. This result fits a second main prediction of the CDS model, since traits targeted by sexual selection show higher sensitivity to condition than in not-sexually selected traits, resulting in more expressed variation under resource stress (Rowe & Houle, 1996). Higher variation in males may occur because differences among individuals in achieving and allocating resources emerge under higher levels of environmental stress (David *et al.*, 2000; Cotton *et al.*, 2004b; Cothran & Jeyasingh, 2010). Furthermore, the magnitude of ecological stress experienced by natural populations strongly impacts condition dependency of sexually selected traits, and could play an important role in shaping trait variation and thus the opportunity for sexual selection (Cothran & Jeyasingh, 2010). Consequently, the difference in the variability of head shape in male compared to the females could be an indicator that island features actually result in resource stress.

Even though no direct measures of habitat features that may potentially represent environmental stressors for the expression of head shape in

lizards has been carried out to date, our data suggested that small island size, low habitat diversity, no human presence and therefore lack of human related habitats, drier and warmer climate regimes might promote reduced intensity of head's shape sexual dimorphism (Figs 3, 7). This pattern is consistent with the hypothesis that unfavourable environmental conditions may actually represent a stress which limits the expression of SD, since common wall lizards are well known to be well adapted to human made habitats (such as buildings and drywalls or olive groves and vineyards) and are generally less thermophilus than other Italian lizards like, e.g., *Podarcis siculus* (Biaggini *et al.*, 2011; Mangiacotti *et al.*, 2013). Thus, the environmental conditions of small islets or islands kept at low habitat diversity may reliably impose more severe limits to lizard survival, and consequently to the allocation of resources in the expression of secondary sexual characters. However, specific researches are needed to achieve a fine ecological characterization of the micro-habitats preferred by insular common wall lizards, as well as to assess the structure and dynamics of the population on their respective islands to better understand how these local parameters influence the morphology and sexual dimorphism of this species.

ACKNOWLEDGEMENTS

We thank Dr. Annamaria Nistri for allowing us to study specimens preserved in the 'La Specola' Zoological Museum (Florence, Italy). We also thank two anonymous referees for their useful comments that sensibly improved a previous version of the ms.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Table S1. List of the 15 environmental variables measured in each island.

Table S2. Summary table of the RDA carried out on the 15 habitat variables in S1 constrained by size, distance from the mainland and genetic clade of islands.

Table S3. Summary table of the linear mixed models we carried out to control for the clustering of data within islands. In these models, the dependent variables were the first five PC scores of head shape, while the predictors included the same fixed structure as in the MANOVAs and a random effect for the islands. We report coefficient for the fixed component only.