



Insularity affects head morphology, bite force and diet in a Mediterranean lizard

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Island environments differ with regard to numerous features from the mainland and may induce large-scale changes in most aspects of the biology of an organism. In this study, we explore the effect of insularity on the morphology and performance of the feeding apparatus, a system crucial for the survival of organisms. To this end, we examined the head morphology and feeding ecology of island and mainland populations of the Balkan green lizard, *Lacerta trilineata*. We predicted that head morphology, performance and diet composition would differ between sexes and habitats as a result of varying sexual and natural selection pressures. We employed geometric morphometrics to test for differences in head morphology, measured bite forces and analysed the diet of 154 adult lizards. Morphological analyses revealed significant differences between sexes and also between mainland and island populations. Relative to females, males had larger heads, a stronger bite and consumed harder prey than females. Moreover, island lizards differed in head shape, but not in head size, and, in the case of males, demonstrated a higher bite force. Islanders had a wider food niche breadth and included more plant material in their diet. Our findings suggest that insularity influences feeding ecology and, through selection on bite force, head morphology. © 2014 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2014, 112, 469–484.

ADDITIONAL KEYWORDS: geometric morphometrics – islands – *Lacerta trilineata* – sexual shape dimorphism.

INTRODUCTION

The feeding apparatus is a form–function complex that is involved in numerous ecological and behavioural activities in addition to feeding (Herrel *et al.*, 2010). It shows an important variation between sexes and among species, probably related to the exploita-

tion of different resources, which may result in a decreased competition for food (Arnold, 1987; Preest, 1994; Verwajen, Van Damme & Herrel, 2002). In addition, sexual dimorphism of the feeding apparatus can lead to significant differences in the size, shape and hardness of prey consumed between the two sexes (Herrel *et al.*, 2001b). Bite force, on the other hand, affects prey-handling efficiency (Herrel *et al.*, 1999, 2001b) and is directly related to the outcome of male–male combat (Lappin, Hamilton & Sullivan,

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2006; Huyghe *et al.*, 2009). The relation between head size and bite force is direct and individuals with bigger heads usually exert higher maximal bite force, as larger heads can accommodate a greater amount of jaw muscles (Herrel, De Grauw & Lemos-Espinal, 2001a; McBrayer & Anderson, 2007; Anderson, McBrayer & Herrel, 2008; Herrel *et al.*, 2010; Kaliontzopoulou *et al.*, 2012). Natural and sexual selection may act simultaneously or sequentially (or even oppose each other) on these traits, governing energy input through shifts in feeding ecology.

The majority of lizards are generalists, feeding on a wide variety of prey items, whereas only a few are true specialists (Greene, 1982; Pianka, 1986; Greer, 1989). Lacertid lizards are prime examples of the former and feed on a range of terrestrial invertebrates (Arnold, 1987; Maragou, Valakos & Chondropoulos, 1997), although some are dedicated omnivores or herbivores (Pérez-Mellado & Corti, 1993; Martin *et al.*, 2005; Vervust *et al.*, 2010). Interestingly, the diet of insular species differs from that of their mainland peers (Gorman, 1979; Pérez-Mellado & Corti, 1993). This should come as no surprise. Insularity affects every aspect of lizard biology, including life history, antipredatory tactics, body size, digestion, thermoregulation and morphology (Pérez-Mellado, Corti & Lo Cascio, 1997; Pafilis *et al.*, 2007, 2011; Herrel *et al.*, 2008; Vervust *et al.*, 2010; Meiri, Raia & Phillimore, 2011; Novosolov, Raia & Meiri, 2013; Sagonas, Valakos & Pafilis, 2013). Feeding ecology represents no exception to this general rule and island lizards show impressive deviations in their diet from their mainland counterparts (Van Damme, 1999; Castilla, Vanhooydonck & Catenazzi, 2008; Castilla & Herrel, 2009; Pafilis *et al.*, 2009). The depauperate island communities impose changes in a lizard's dietary niche and often lead to the utilization of novel resources. As such, insularity may constitute a powerful driver of evolution (Grant & Grant, 2011).

Most feeding ecology studies in lacertid lizards have been conducted at the species level and have focused on different island endemics (e.g. Sadek, 1981; Adamopoulou, Valakos & Pafilis, 1999; Lo Cascio & Pasta, 2006; Castilla, Herrel & Gosá, 2009; Pérez-Mellado *et al.*, 2011). Although of interest, these studies suffer the effects of phylogenetic constraints and, consequently, data independence when placed in a broader, comparative context (Garland & Adolph, 1994; Losos & Miles, 1994). Studies at the intraspecific level could provide evidence of adaptive divergence because of the particular nature of island habitats, although the effect of phylogenetic independence should be resolved even in the case of single species populations. However, very few studies comparing directly the diet of mainland and island popu-

lations have been conducted within a single species (Luiselli, Filippi & Capula, 2005; Perera *et al.*, 2006; Dutra *et al.*, 2011).

Here, we explore the effects of insularity on the morphology and performance of the feeding apparatus in a lacertid lizard. We focused on head shape and size, bite force, and diet in the Balkan green lizard *Lacerta trilineata*, which is distributed in both continental and insular Greece (Valakos *et al.*, 2008). Islands host less diversified and less abundant prey communities (Pérez-Mellado & Corti, 1993; Brown & Perez-Mellado, 1994). However, head morphology and performance are related to prey consumption (Herrel *et al.*, 1999, 2001b). We predicted that, if food availability differs between mainland and islands, head morphology and bite force would also be different. Given that, in lacertids, most species are dimorphic, we investigated variation in both sexes. We formulated three hypotheses. First, we anticipated that males would have larger heads and higher bite forces than females, following the typical pattern of sexual dimorphism in lacertid lizards (Braña, 1996; Herrel, Van Damme & De Vree, 1996; Scharf & Meiri, 2013). Second, we predicted that island populations would differ in terms of diet composition from their mainland counterparts because of the particular structure of insular communities and differences in food availability (Carretero, 2004; Pafilis, Valakos & Foufopoulos, 2005; Herrel *et al.*, 2008). Third, we predicted that head dimensions and bite force would be different in insular versus mainland populations because of the different selection pressures imposed by an altered dietary regime on islands.

MATERIAL AND METHODS

STUDY SPECIES

The Balkan green lizard is a large-bodied lacertid [adult snout to vent length (SVL) of up to 17 cm] that includes a wide variety of invertebrates and, occasionally, small lizards and rodents into its diet (Arnold, 1987). The distribution of the species covers the southern Balkans, including Greece, where it can be found throughout the mainland and on islands, in almost all types of habitat (Valakos *et al.*, 2008).

One hundred and fifty-four adult individuals from continental and island populations were measured: 20 females and 48 males from the islands (Crete: nine females and 20 males; Andros: five females and 14 males; Skyros: six females and 14 males) and 30 females and 56 males from the mainland (Epirus: 10 females and 10 males; Thessalia: eight females and 22 males; Peloponnese: 12 females and 24 males) (Supporting Information, Fig. S1). The majority of the specimens (105 lizards) were deposited at the

Herpetological Collection of the Natural History Museum of Crete. The rest (49 individuals: 25 males and 24 females) were captured in the field in accordance with Greek National Law (Presidential Decree 67/81) and were held at the laboratory facilities of the Biology Department at the University of Athens. Lizards were housed individually in plastic terrarium ($80 \times 30 \times 40 \text{ cm}^3$) under a controlled photoperiod (12 h light : 12 h dark), fed every other day with adult crickets and mealworms, coated with mineral powder (TerraVit Powder, JBL GmbH & Co. KG), and had access to water *ad libitum*.

HEAD SIZE AND SHAPE

Five linear head characters were measured for each lizard: head length (HL), measured from the tip of the snout to the posterior border of the collar, head width (HW), measured at the widest part of the head, head height (HH), measured at the highest part of the head, pileus length (PL), measured from the tip of the snout to the posterior scale of the head, and jaw length (JL) (Fig. 1). SVL was also recorded as an index of body size. All length measurements were taken in duplicate (we used the average value) using a digital caliper (Silverline 380 244, accurate to 0.01 mm).

Dorsal and lateral head shapes were quantified and analysed using geometric morphometric approaches

(Rohlf & Marcus, 1993; Klingenberg, 2010). The MorphoJ software package was used for analyses (Klingenberg, 2011). Geometric morphometric analyses can detect even small morphological differences between groups and are thus especially appropriate for intraspecific studies (Kaliontzopoulou, Carretero & Liorentel, 2007). In our study, we selected 30 landmarks in the dorsal view and 16 in the lateral view of the head (Fig. 1) (for details of the landmarks, see Kaliontzopoulou *et al.*, 2007). We used landmarks that are good descriptors of head shape (Kaliontzopoulou *et al.*, 2007; Bruner & Costantini, 2009; Huyghe *et al.*, 2009). Heads were photographed with a digital camera (Panasonic DMC-FS41, resolution 14 MP) attached in a tripod from a distance of 15 cm, using a grid as a background for scaling. Photographs were digitized with the help of TpsDig software (Rohlf, 2008a). To quantify the dorsal shape, we averaged symmetric landmarks on left and right sides along the mid-line (Kaliontzopoulou *et al.*, 2007). Finally, to visualize the differences in geometric head shape between groups, we used Morpheus software (Slice, 1999).

BITE FORCE

Bite force was measured *in vivo* using a Kistler force transducer (type 9203, Kistler Inc., Winterthur, Switzerland) mounted on a purpose-built holder and

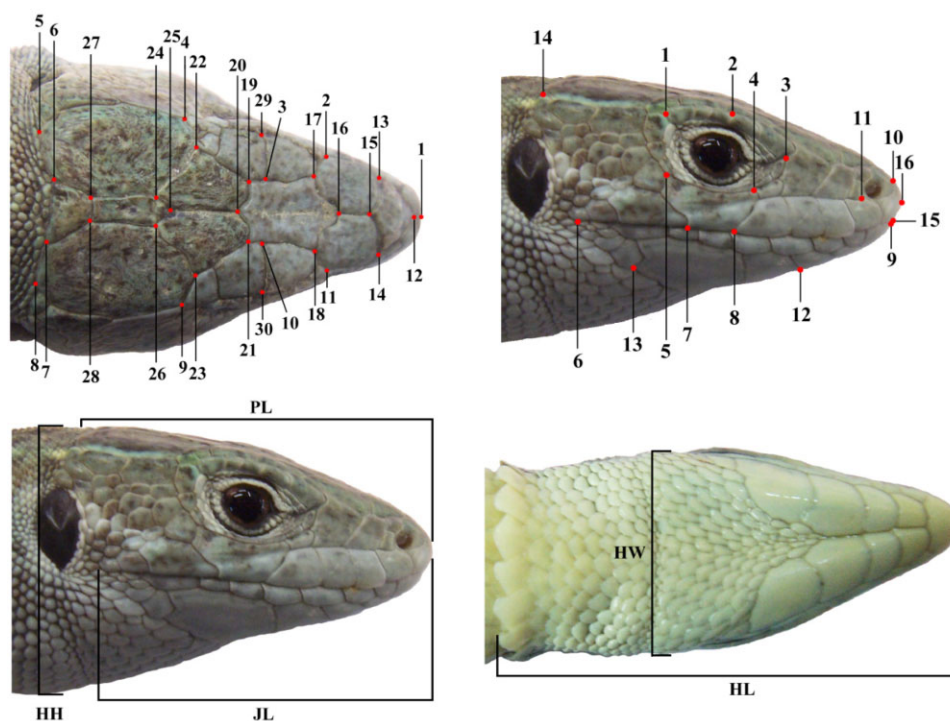


Figure 1. The five linear head measurements taken and landmarks used in the geometric analysis, in dorsal and lateral view. Head length (HL), head height (HH), head width (HW), jaw length (JL) and pileus length (PL).

connected to a Kistler charge amplifier (type 5995A, Kistler Inc.). To quantify bite force, lizards were induced to bite a pair of thin metal plates connected to the force transducer (for a more detailed description, see [Herrel *et al.*, 1999](#)). Before performing bite experiments, lizards were allowed to thermoregulate for 1 h, in order to obtain their preferred body temperature. Each lizard was tested three times ([Herrel *et al.*, 2010](#)). The highest value obtained during the tests for each individual was considered to be the maximal bite force that a lizard could achieve, and was retained for further analyses.

DIET COMPOSITION AND PREY CHARACTERISTICS

We dissected 105 specimens, removed the digestive tract and examined the prey remnants. We also collected the faecal material from an additional 49 specimens and analysed it under a binocular dissecting microscope. Previous studies have shown that faeces sample analyses provide similar results to stomach content analyses ([Capula & Luiselli, 1994](#); [Angelici, Luiselli & Rugiero, 1997](#); [Perez-Mellado *et al.*, 2011](#); but see [Pincheira-Donoso, 2008](#)). Prey items were identified to order level, whereas the length and width of intact prey, when possible, were measured to the nearest 0.5 mm with an ocular eyepiece.

Prey items were also classified on the basis of their hardness and flying ability. Hardness was determined on the basis of previous studies ([Herrel *et al.*, 2001b](#); [Verwajen, Van Damme & Herrel, 2002](#)) and followed the categorization by [Vanhooydonck, Herrel & Van Damme \(2007\)](#). Coleoptera, Gastropoda, Isopoda, Hymenoptera and Formicidae were considered as hard prey, Orthoptera, Haplotaxida, Homoptera, Hemiptera, Diplopoda and Chilopoda were classified as being of intermediate hardness, and Aranae, Opiliones, Dermaptera, Diptera, Lepidoptera, Trichoptera and Larvae were characterized as soft prey. Moreover, based on the escape potential of prey, we classified Diptera, Lepidoptera, Hymenoptera and Orthoptera as evasive prey and the remaining Orders as sedentary. Members of Formicidae were separated from the rest of Hymenoptera in subsequent analyses, because of their inability to fly.

STATISTICAL ANALYSES

The Kolmogorov–Smirnov and Lilliefors tests were used to examine the normality of the data. Whenever parametric assumptions were violated, non-parametric tests were performed. We used a two-way multivariate analysis of variance (MANOVA) to test for differences in morphological traits, with habitat (mainland and island, HAB), sex (SEX) and their interaction as fixed effects. The two-way MANOVAs

were followed by the *post hoc* Tukey honestly significant difference (HSD) test. As a complementary approach, to reduce the within-group error caused by the effect of SVL, we also conducted multivariate analysis of covariance (MANCOVA) using the biometric variables. In addition, in order to further explore the variation in morphological traits, we performed regression analyses with all five head dimensions on one side and body size (SVL) and total head size (HS) on the other. The geometric HS was estimated as the third root of HL times HW times HH ([Mosimann, 1970](#); [Kaliontzopoulou *et al.*, 2012](#)). Finally, we evaluated the effects of linear traits (SVL, HS and head dimensions) on bite force (dependent variable) performing a MANCOVA, with HAB, SEX and their interaction as fixed effects.

In the geometric morphometric analyses, we first performed a full Procrustes fit in MorphoJ 1.05b ([Klingenberg, 2011](#)) to remove size and position effects and to keep only geometric shape ([Dryden & Mardia, 1998](#)). We then conducted a discriminant analysis using the new matrix that was created after the Procrustes fit, employing a canonical variate analysis (CVA) for the dorsal and lateral side of the head, with the effects of HAB, SEX and their interaction as fixed effects. Procrustes ANOVA was used for both sides to quantify the relative amounts of variation between groups ([Klingenberg & McIntyre, 1998](#); [Klingenberg, Barluenga & Meyer, 2002](#)). However, because of the limitations of the Procrustes ANOVA in MorphoJ, centroid size values were also estimated in tpsRelw ([Rohlf, 2008b](#)), and the values obtained were used in further statistical analysis as shape variables.

The diet composition of each group of *L. trilineata* was summarized in two ways: as the percentage of the total number of prey items in the diet (%N) and as the percentage of individuals eating a prey taxon (*f*). Niche breadth (*H'*) was calculated using the Shannon–Wiener diversity index ([Krebs, 1998](#)), whereas a *t*-test was performed to obtain differences among the diversity index of groups ([Zar, 2010](#)). As the Shannon index is largely affected by the most abundant species, we also calculated the Jaccard index ([Jaccard, 1908](#)) to test the similarity in diet composition. We also used Pianka's overlap index (Q_{jk}) to obtain a quantitative measure of food niche similarity among groups ([Pianka, 1975](#)). To further investigate the functional properties of prey items (hardness and flying), we tested whether the proportions of hard and flying prey were significantly different among SEX and HAB using χ^2 test. We also tested whether prey size differed among groups, taking into account the interaction of HAB \times SEX. Finally, in order to test how morphology and diet composition were associated with each other, we

performed a two-way Mantel test with 10 000 permutations using the Mahalanobis distance matrix for morphology (lateral head shape) on one side and the divergence niche matrix (1 – niche overlap), representing the diet variation among groups, on the other. Correlation analyses were performed between bite force and body size with the mean prey size of each individual.

RESULTS

VARIATION IN HEAD SIZE

The three island populations were pooled for the subsequent analyses as no differences were observed in head dimensions (ANOVA, Tukey HSD: females, all $P > 0.05$; males, all $P > 0.05$). Similarly, we grouped the three mainland populations as head traits did not differ (ANOVA, Tukey HSD: females, all $P > 0.05$; males, all $P > 0.05$).

All head dimensions (HL, HH, HW, PL and JL) differed significantly between the two sexes (two-way MANOVA, Wilks' lambda = 0.97, $F_{5,146} = 1.00$, $P > 0.05$; *post hoc* Tukey HSD test, $P < 0.05$, Fig. 2). Furthermore, males had significantly larger SVL than females (two-way ANOVA, $F_{1,150} = 0.56$, $P > 0.05$; *post hoc* Tukey HSD test, Table 1). As a result of the effect of body size on head traits, we repeated the MANOVA mentioned above, with SVL as a covariate, and the differences remained (MANCOVA, Wilks' lambda = 0.97, $F_{5,145} = 0.89$; *post hoc* Tukey's HSD

test, $P < 0.05$, Table 1). In all cases, pairwise analyses showed that males were significantly larger than females (Table 1, Fig. 2).

No differences were found within sexes regarding head dimensions. Mainland and island males and females did not differ (two-way MANCOVA, Wilks' lambda = 0.97, $F_{5,145} = 0.892$, $P > 0.05$; *post hoc* Tukey HSD test, $P > 0.05$, Table 1). Similarly, head size also showed no significant differences between populations of the same sex (ANOVA, $F_{1,150} = 0.26$, $P > 0.05$; *post hoc* Tukey HSD test, $P > 0.05$, Table 1). Finally, SVL was similar for mainland and island populations (ANOVA, $F_{1,150} = 0.56$, $P > 0.05$; *post hoc* Tukey HSD test, $P > 0.05$, Table 1).

The results of regression analyses of the morphological traits indicated a strong positive correlation between all pairs of head variables, as well as between all head traits and SVL, in both sexes (Fig. 3). The comparison of regression coefficients of all head variables among the four groups yielded significant differences between the sexes, but not between populations, with males demonstrating a more rapid increase in head traits than females with respect to body size (all $P < 0.05$).

VARIATION IN HEAD SHAPE AND BITE FORCE

Procrustes ANOVAs with pairwise comparison on both the lateral and dorsal head projections showed a significant difference in the interaction of HAB × SEX

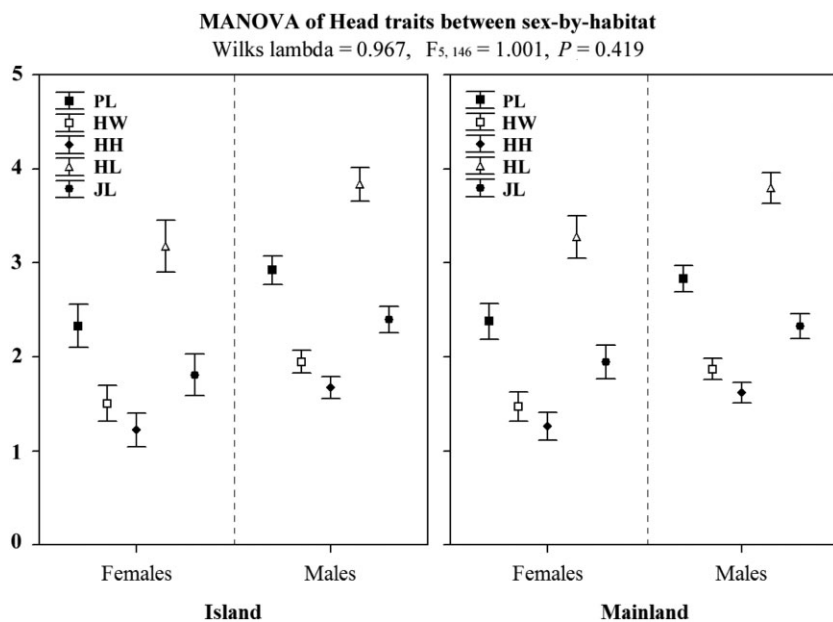


Figure 2. Multivariate analysis of variance (MANOVA) results for head biometric traits (in cm) for the four groups (island males, island females, mainland males and mainland females). Points represent the means and vertical bars the standard error. Open triangles represent head length (HL), filled diamonds head height (HH), open squares head width (HW), filled circles jaw length (JL) and filled squares pileus length (PL).

Table 1. Results of the different statistical analyses and descriptive statistics for the five head linear traits, HL (head length), HH (head height), HW (head width), PL (pileus length) and JL (jaw length), as well as SVL (snout to vent length, body size) and HS (head size). All morphological traits are given in centimetres. The mean \pm 1SD, sample size (*N*) and range (minimum–maximum) are presented for each parameter. GM refers to geometric morphometric (for both the lateral and dorsal projections) analyses

Habitat	Sex	SVL	HL	HH	HW	PL	JL	HS	GM
Island (I)	Males (M)	12.15 \pm 2.06 (8.5–16.0) <i>N</i> = 48	3.83 \pm 0.65 (2.62–5.41) <i>N</i> = 48	1.67 \pm 0.49 (0.96–2.81) <i>N</i> = 48	1.94 \pm 0.51 (1.17–3.25) <i>N</i> = 48	2.93 \pm 0.59 (2.0–4.19) <i>N</i> = 48	2.4 \pm 0.49 (1.56–3.39) <i>N</i> = 48	2.31 \pm 0.54 (1.43–3.53) <i>N</i> = 48	<i>N</i> = 48
	Females (F)	10.76 \pm 1.97 (8.0–14.8) <i>N</i> = 20	3.18 \pm 0.69 (2.19–4.53) <i>N</i> = 20	1.22 \pm 0.25 (0.9–1.66) <i>N</i> = 20	1.51 \pm 0.32 (1.08–2.02) <i>N</i> = 20	2.33 \pm 0.41 (1.7–3.18) <i>N</i> = 20	1.81 \pm 0.37 (1.27–2.56) <i>N</i> = 20	1.80 \pm 0.37 (1.31–2.47) <i>N</i> = 20	<i>N</i> = 20
Mainland (M)	Males (M)	11.60 \pm 2.15 (8.0–17.4) <i>N</i> = 56	3.79 \pm 0.64 (2.74–6.16) <i>N</i> = 56	1.62 \pm 0.44 (0.87–2.84) <i>N</i> = 56	1.87 \pm 0.46 (1.02–3.05) <i>N</i> = 56	2.83 \pm 0.58 (1.8–4.44) <i>N</i> = 56	2.32 \pm 0.61 (1.43–4.52) <i>N</i> = 56	2.25 \pm 0.53 (1.36–3.76) <i>N</i> = 56	<i>N</i> = 56
	Females (F)	10.73 \pm 1.58 (8.46–15.2) <i>N</i> = 30	3.27 \pm 0.51 (2.46–5.17) <i>N</i> = 30	1.26 \pm 0.28 (0.88–2.41) <i>N</i> = 30	1.47 \pm 0.27 (1.04–2.62) <i>N</i> = 30	2.38 \pm 0.35 (1.9–3.8) <i>N</i> = 30	1.95 \pm 0.32 (1.45–3.13) <i>N</i> = 30	1.82 \pm 0.32 (1.35–3.2) <i>N</i> = 30	<i>N</i> = 30
Statistical analyses (two-way)		ANOVA, $F_{1,150} = 0.56$, $P = 0.455$	MANCOVA, Wilks' lambda = 0.970, $F_{5,145} = 0.892$, $P = 0.488$					ANOVA, $F_{1,150} = 0.26$, $P = 0.606$	ANOVA, $P < 0.05$
Groups (pairwise)		{IM,MM} {IF,MF}	{IM,MM} {IF,MF}	{IM,MM} {IF,MF}	{IM,MM} {IF,MF}	{IM,MM} {IF,MF}	{IM,MM} {IF,MF}	{IM,MM} {IF,MF}	{IM}{MM} {IF}{MF}

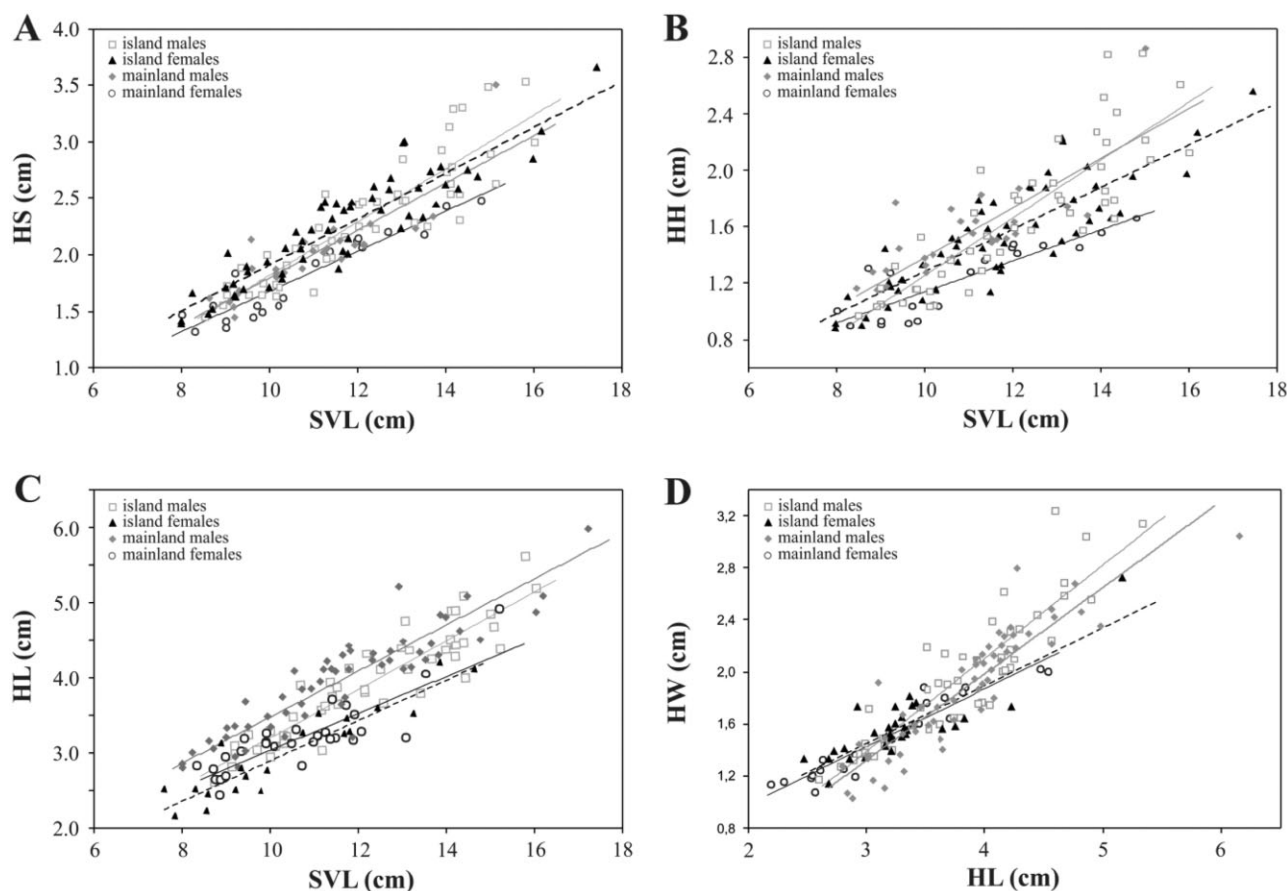


Figure 3. Allometric relationships between body size (snout to vent length, SVL) and head size (HS) (A), head height (HH) (B) and head length (HL) (C), and between head width (HW) and HL (D), for the four groups (island males, island females, mainland males and mainland females). Open grey squares, full grey line, island males; filled black triangles, broken black line, island females, filled grey diamonds, full dark grey line, mainland males; open black circles, full black line, mainland females.

(Procrustes ANOVA, all $P < 0.05$, Table 1, Fig. 4). This pattern was confirmed by discriminant analysis on both head projections (Klingenberg, 2011). Males had more rounded, wider and taller heads than females, whereas island populations had more elongated and taller heads, but similar HWs, in comparison with their mainland counterparts (Fig. 5). Pairwise comparisons of centroid size values, which were extracted from tpsRelw software (Rohlf, 2008b), confirmed the aforementioned patterns (two-way ANOVA, lateral projection: $F_{3,150} = 19.18$, $P < 0.05$, Tukey HSD, $P < 0.05$; dorsal projection: $F_{3,150} = 19.85$, $P < 0.05$, Tukey HSD, $P < 0.05$).

Bite force differed significantly between sexes in both island and mainland habitats. Males demonstrated higher absolute maximum bite force than females (two-way ANCOVA, $F_{1,44} = 3.57$, $P > 0.05$; *post hoc* Tukey HSD test, all $P < 0.05$; Table 2). When HH, HW, HS and SVL were taken into account, the differences remained (MANCOVA, *post hoc* Tukey HSD

test, $P < 0.05$). Significant differences were also found between mainland and island males (the latter had a stronger bite), but not between females (two-way ANCOVA, *post hoc* Tukey HSD test, $P < 0.05$, Table 2). After taking into account the head variables, the differences remained (MANCOVA, *post hoc* Tukey HSD test, $P < 0.05$). Finally, the regression coefficients of bite force and linear traits were significantly different between males and females. All males demonstrated a higher slope for bite force with increasing head measures (all $P < 0.05$, Fig. 6).

VARIATION IN DIET COMPOSITION AND PREY CHARACTERISTICS

The comparison between the two different methods (faecal pellets vs. stomach contents) showed no significant differences in prey composition (the overlap between the two methods was greater than 90% for the four groups, all $P > 0.05$), and thus we pooled the

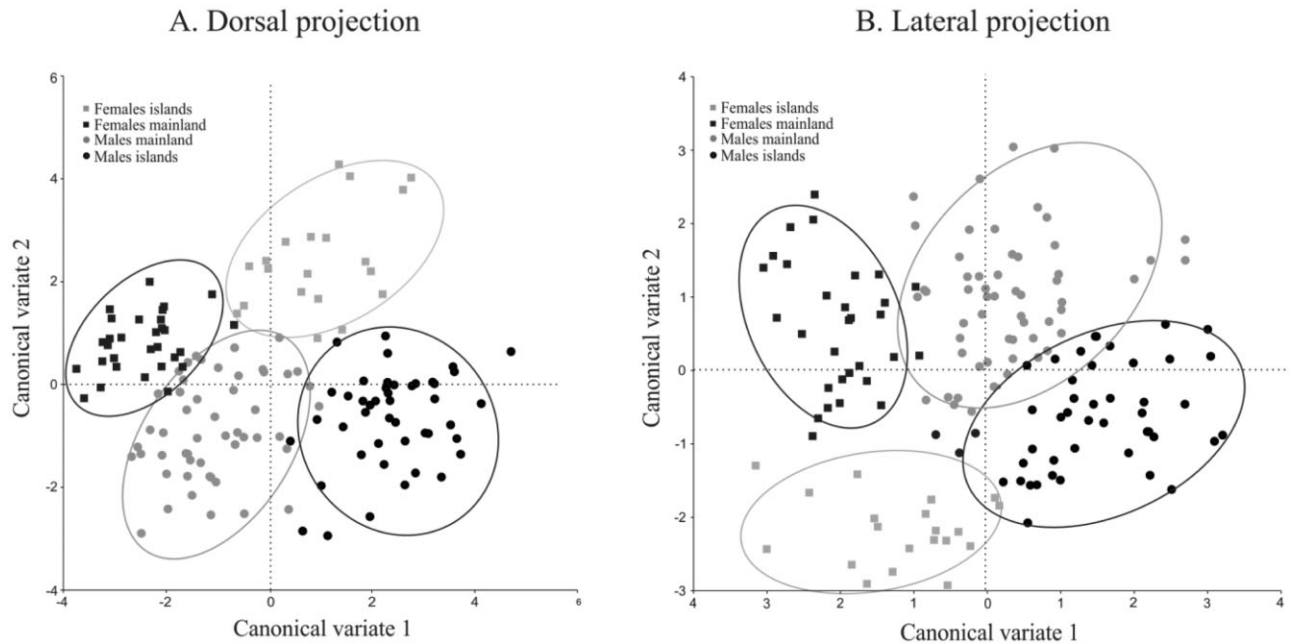


Figure 4. Canonical variance analysis of the geometric morphometric data of the head in dorsal (A) and lateral (B) views. Grey squares, island females; black squares, mainland females; grey circles, mainland males; black circles, island males.

results. χ^2 test for the most common prey items yielded no statistically significant differences (χ^2 test, Fisher's exact $P > 0.05$), and thus island populations were pooled into two groups (one for each sex). The same occurred for the three mainland populations.

The diet of *L. trilineata* is composed mainly of arthropods, with most frequent prey groups (f) being Coleoptera, Orthoptera and Isopoda (Fig. 7). Island lizards, of both sexes, had wider food niche breadth than their mainland counterparts (males H' : islands = 1.972 vs. mainland = 1.358; t -test, $t = 5.34$, d.f. = 542.96, $P < 0.05$; females H' : islands = 1.889 vs. mainland = 1.584; t -test, $t = 2.09$, d.f. = 188.06, $P < 0.05$). However, there were no differences between the sexes derived from the same habitat with regard to food niche breadth (island H' : males vs. females; t -test, $t = 0.59$, d.f. = 174.52, $P > 0.05$; mainland H' : males vs. females; t -test, $t = 1.86$, d.f. = 440.78, $P > 0.05$). The Jaccard similarity index denoted significant differences in the diet composition between mainland and island populations and between males and females (in all pairwise comparisons, the Jaccard similarity index was approximately 0.6).

The proportion of hard prey items was significantly higher in males than in females in both island and mainland lizards (χ^2 test, Fisher's exact $P < 0.05$). However, mainland lizards consumed a higher proportion of hard prey relative to island lizards (χ^2 test, Fisher's exact $P < 0.05$). The proportion of evasive prey was significantly higher only in the case of

island females compared with the rest of the groups (χ^2 test, Fisher's exact $P < 0.05$) (Fig. 7). Mean prey size was positively correlated with body size ($r = 0.54$, $P < 0.05$) and bite force ($r = 0.53$, $P < 0.05$) (Fig. 7). However, mean prey size (based on the most common prey; Coleoptera, Isopoda, Formicidae, Hymenoptera, Larvae and Orthoptera) showed no differences between groups (ANOVA, $F_{3,150} = 2.13$, $P > 0.05$; Fig. 7). Finally, island lizards included more plant material in their diet than their mainland counterparts (for both sexes, χ^2 test, Fisher's exact $P < 0.05$; Fig. 7). The Mantel test associating food preferences with lateral head shape indicated a positive correlation between lateral head shape and diet ($r = 0.71$, $P < 0.05$), but not between dorsal head shape and diet composition ($r = 0.59$, $P > 0.05$).

DISCUSSION

The results of our analyses corroborate the typical pattern of sexual dimorphism observed in lacertid lizards, with males having bigger heads and greater bite forces than females (Herrel *et al.*, 2001b; Verwajen *et al.*, 2002; Kaliontzopoulou *et al.*, 2012). The comparison between mainland and island populations also yielded interesting differences. There was a clear distinction in linear head dimensions between males and females, supporting our first hypothesis. In accordance with our second hypothesis, island lizards demonstrated wider dietary niche breadth compared

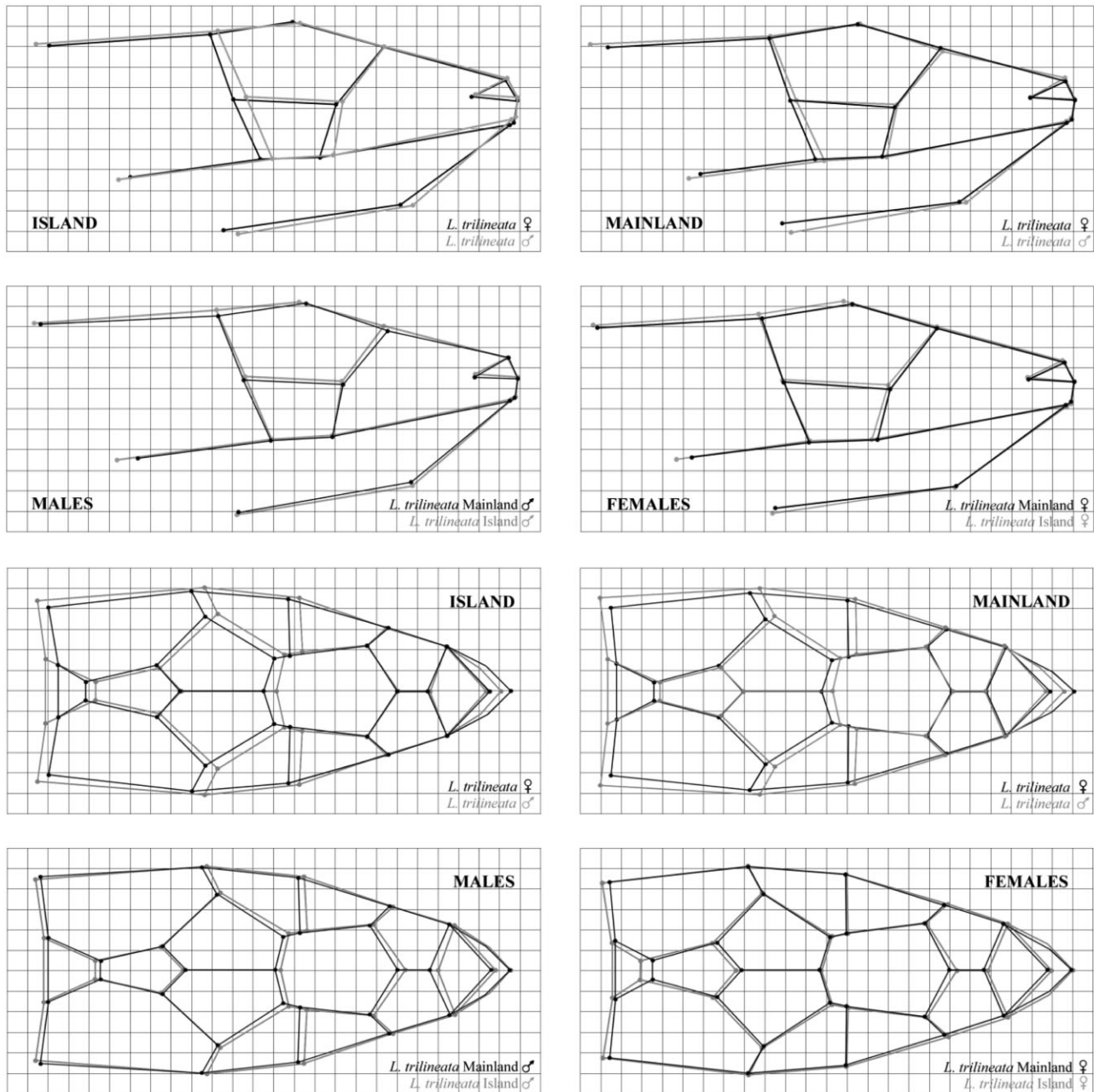


Figure 5. Comparison of head shape between males and females and between island and mainland individuals in lateral and dorsal views.

with their mainland conspecifics. Our last hypothesis was not fully confirmed: although head shape differed between island and mainland lizards, head size did not. Bite force showed a significant difference only in the case of insular males, which showed a harder bite than their mainland counterparts.

Males had larger SVL and more robust heads (Table 1, Fig. 2), and greater correlation coefficients than females for all linear measurements relative to SVL (Fig. 3). Our geometric morphometric analyses

also indicated a distinct sexual shape dimorphism in dorsal and lateral view, confirming our initial hypothesis. Males had more rounded, wider and taller heads (Fig. 5). This pattern is quite common in lacertid species (Verwajen *et al.*, 2002; Lappin *et al.*, 2006; Kaliontzopoulou, Carretero & Llorente, 2008; Herrel *et al.*, 2009; Kaliontzopoulou *et al.*, 2012) and is consistent with sexual selection (Abouheif & Fairbairn, 1997). Given that head dimensions and, in particular, HH and HW, are associated with bite force, the

Table 2. Results of statistical analyses and descriptive statistics for the linear traits of lizards for which the bite force was measured. HL (head length), HH (head height), HW (head width), PL (pileus length); JL (jaw length), SVL (snout to vent length) and HS (head size). All morphological traits are given in centimetres. The mean \pm 1SD, sample size (*N*) and range (minimum–maximum) are presented for each parameter. BF refers to bite force and is measured in Newtons (N). In the case of the pairwise comparison on bite force, all head traits given in the table were used as covariates and the grouping pattern observed was identical

Habitat	Sex	SVL	PL	HH	HW	HL	JL	HS	BF
Island (I)	Males (M)	13.97 \pm 1.26 (11.39–15.8) <i>N</i> = 12	3.46 \pm 0.52 (2.53–4.19) <i>N</i> = 12	2.14 \pm 0.46 (1.52–2.81) <i>N</i> = 12	2.40 \pm 0.56 (1.64–3.25) <i>N</i> = 12	4.32 \pm 0.55 (3.54–5.41) <i>N</i> = 12	2.85 \pm 0.42 (2.19–3.39) <i>N</i> = 12	2.61 \pm 0.51 (1.85–3.33) <i>N</i> = 12	66.43 \pm 12.41 <i>N</i> = 12
	Females (F)	12.03 \pm 1.34 (10.3–14.8) <i>N</i> = 12	2.61 \pm 0.25 (2.16–3.03) <i>N</i> = 12	1.41 \pm 0.53 (1.04–1.66) <i>N</i> = 12	1.72 \pm 0.25 (1.37–2.32) <i>N</i> = 12	3.58 \pm 0.41 (2.9–4.47) <i>N</i> = 12	2.10 \pm 0.25 (1.55–2.56) <i>N</i> = 12	1.85 \pm 0.18 (1.45–2.17) <i>N</i> = 12	39.43 \pm 7.98 <i>N</i> = 12
Mainland (M)	Males (M)	12.83 \pm 2.06 (10.36–17.4) <i>N</i> = 13	3.16 \pm 0.54 (2.45–4.44) <i>N</i> = 13	1.92 \pm 0.41 (1.47–2.84) <i>N</i> = 13	2.16 \pm 0.39 (1.65–3.05) <i>N</i> = 13	4.17 \pm 0.69 (3.41–6.16) <i>N</i> = 13	2.61 \pm 0.59 (1.77–3.68) <i>N</i> = 13	2.36 \pm 0.43 (1.85–3.37) <i>N</i> = 13	55.98 \pm 11.41 <i>N</i> = 13
	Females (F)	11.65 \pm 1.65 (9.69–15.2) <i>N</i> = 12	2.54 \pm 0.43 (2.19–3.8) <i>N</i> = 12	1.41 \pm 0.36 (1.06–2.41) <i>N</i> = 12	1.62 \pm 0.33 (1.29–2.62) <i>N</i> = 12	3.53 \pm 0.62 (2.91–5.17) <i>N</i> = 12	2.07 \pm 0.39 (1.56–3.13) <i>N</i> = 12	1.80 \pm 0.37 (1.47–2.88) <i>N</i> = 12	39.08 \pm 7.68 <i>N</i> = 12
Statistical analyses (two-way)		ANOVA, $F_{1,45} = 0.67$, $P = 0.417$	Wilks' lambda = 0.895, $F_{5,41} = 0.444$, $P = 0.815$	{IM,MM} {IF,MF}	{IM,MM} {IF,MF}	{IM,MM} {IF,MF}	ANOVA, $F_{1,45} = 0.73$, $P = 0.395$	ANOVA, $F_{1,44} = 3.57$, $P = 0.06$	ANCOVA, $F_{1,44} = 3.57$, $P = 0.06$
Groups (pairwise)		{MM,IF,MF} {IM}	{IM,MM} {IF,MF}	{IM,MM} {IF,MF}	{IM,MM} {IF,MF}	{IM,MM} {IF,MF}	{IM,MM} {IF,MF}	{IM,MM} {IF,MF}	{IM,MM} {IF,MF}

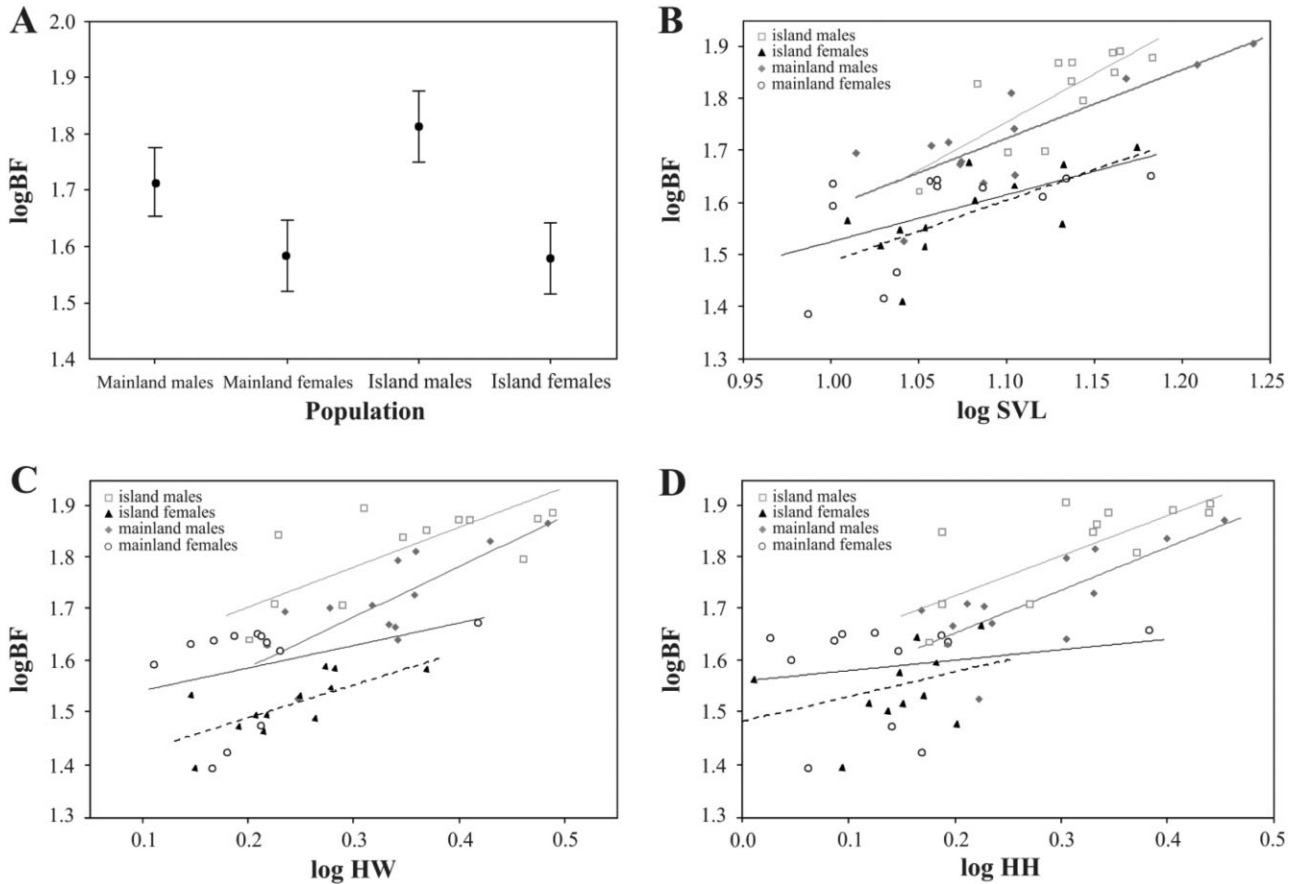


Figure 6. Variation in bite force (BF) and allometric relationships between BF, head dimensions and body size. A, Variation in BF (mean \pm SD). Relationships between BF and body size (snout to vent length, SVL) (B), BF and head width (HW) (C) and BF and head height (HH) (D). Open grey squares, full grey line, island males; filled black triangles, broken black line, island females; filled grey diamonds, full dark grey line, mainland males; open black circles, full black line, mainland females.

observed differences give evidence of sexual selection (Herrel *et al.*, 1996, 1999; Lappin *et al.*, 2006; Brecko *et al.*, 2008; Kaliontzopoulou *et al.*, 2008). The relative increase in these two traits, HH and HW, and the morphological differentiation observed, probably allows males to develop a greater volume (and thus cross-sectional area) of jaw adductor muscles and may also enhance the mechanical advantage of the muscles (Herrel *et al.*, 2001b; Lappin & Husak, 2005; Lappin *et al.*, 2006).

The pattern of sexual dimorphism applied to bite force as well, with males of *L. trilineata* biting harder than females (Table 2). The higher regression slopes relating bite force with SVL, HH, HW and HL in males (Fig. 6) suggest a strong male-biased selection on bite force (Herrel *et al.*, 2010). After correcting for body size and head dimensions, the differences in bite force between sexes remained (Table 2), suggesting additional differences in muscle architecture independent of overall head size and shape. Larger heads

and higher bite forces are advantageous in males for territorial defence, and may affect both mating success and food partitioning (Braña, 1996; Herrel *et al.*, 1999; Kwiatkowski & Sullivan, 2002; Perry *et al.*, 2004; Lappin & Husak, 2005).

With regard to diet composition, *L. trilineata* appears to be a generalist predator, showing a high food niche breadth (H'), in agreement with the only other study on the feeding ecology of the species (Mollov & Petrova, 2013). The feeding ecology of *L. trilineata* resembles that of other large-bodied green lizards, such as *Timon lepidus* or *L. bilineata* (Castilla, Bauwens & Llorente, 1991; Hödar, Campos & Rosales, 1996; Angelici *et al.*, 1997). Coleoptera, Isopoda and Orthoptera were the predominant prey items in both mainland and island populations (Fig. 7). Male lizards from both mainland and islands ate harder prey (e.g. Isopoda, Coleoptera, Gastropoda) than females. To the contrary, females included greater proportions of soft and evasive prey in their

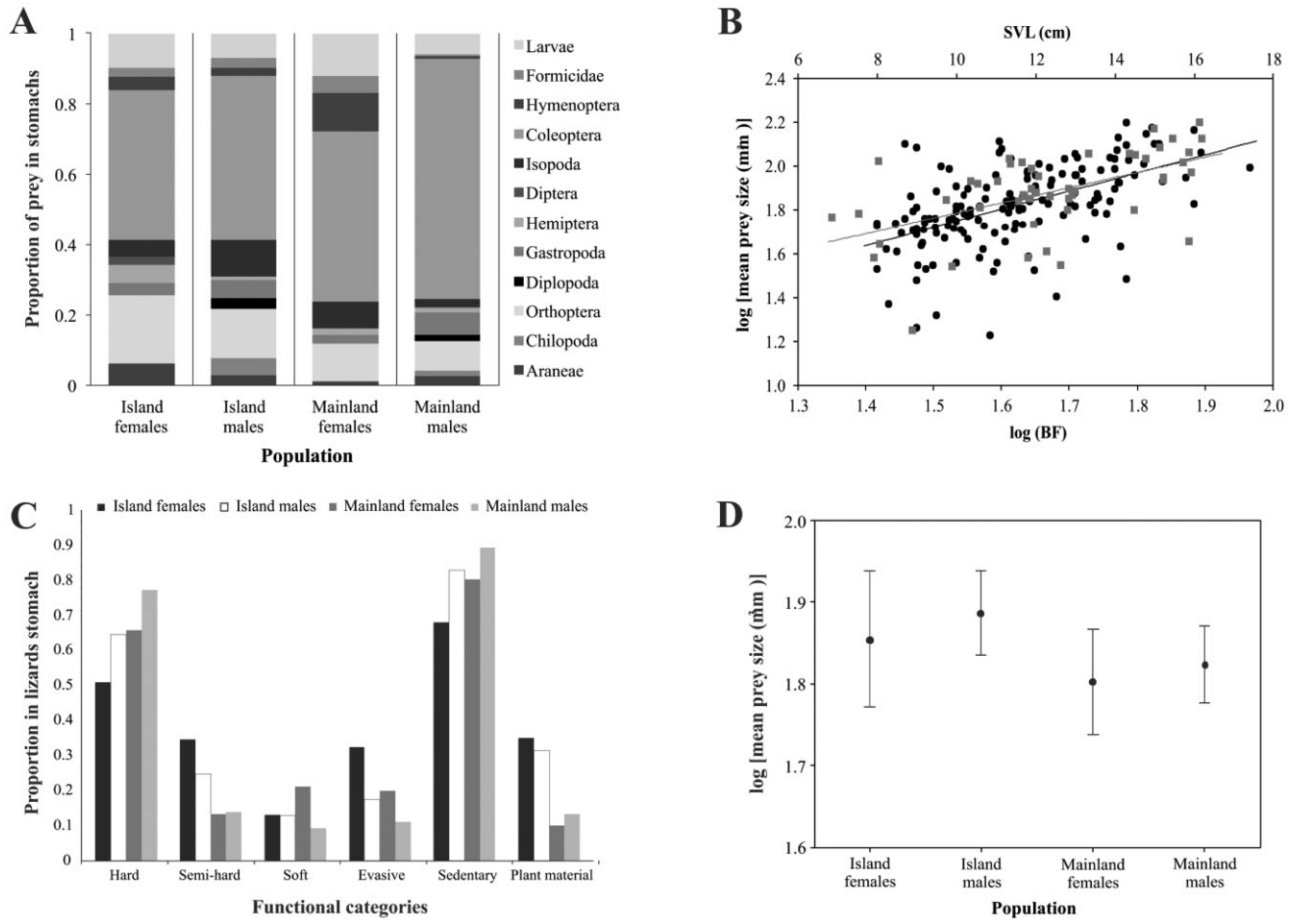


Figure 7. Diet composition in *Lacerta trilineata*. A and B present only the taxonomic groups that exceed 1% of the overall stomach content. A, Proportion of prey taxa (N). B, Relationship between body size (snout to vent length, SVL) and maximum bite force (BF) with mean prey size (filled grey squares, grey line, SVL; filled black circles, black line, BF). C, Proportion of prey hardness, evasive or sedentary taxa and plant material. D, The mean prey size (based on the most common prey; Coleoptera, Isopoda, Larvae, Formicidae, Hymenoptera and Orthoptera) between the four groups.

diet (e.g. Larvae, Araneae, Diptera) (Fig. 7A, C). Despite the larger body size of males, there was no difference between the two sexes in the selection of prey size (Fig. 7D). Dietary niche breadth values were similar for males and females from the same habitat. However, our results demonstrated differences between male and female diets (harder prey), a finding that contradicts previous studies (Castilla *et al.*, 1991; Hödar *et al.*, 1996). As the ability to feed on hard prey requires greater bite forces (Herrel *et al.*, 1999), the higher bite force in males supports the observed consumption of harder prey items.

Island lizards showed higher H' values than mainland ones. A decrease in food abundance, typical of islands, is known to result in a decrease in dietary specialization (Schoener, 1971; Stephens & Krebs, 1986). The food scarcity prevailing in the Mediterr-

anean islands (Pérez-Mellado & Corti, 1993) offers little choice to insular lizards, which have to take advantage of every available food resource to survive. Thus, insular lizards are expected to broaden their diets to compensate for limited food availability (Cooper & Vitt, 2002). Island populations of *L. trilineata* contained more plant material in their diet than their mainland counterparts (Fig. 7C). This tendency of island lizards has been repeatedly described and has been attributed to the scarcity of food resources on islands (Pérez-Mellado & Corti, 1993; Van Damme, 1999).

Our results failed to render full support to the third hypothesis. Although our assumption for differences in head morphology between mainland and island populations was verified, this pattern was only partially applied to bite force. Male island lizards did bite

harder than their mainland kin, but no difference was detected between females from islands relative to those on the mainland (Table 2). In conjunction, head size also did not differ between individuals of the same sex from the two habitats (mainland and islands), with lizards from the islands having similar head dimensions relative to the mainland populations. However, the shape of the head, an important factor that may facilitate access to different resources in different habitats, through its effect on bite force (Vanhooydonck & Van Damme, 1999; Herrel *et al.*, 2001b; Kaliontzopoulou, Carretero & Llorente, 2010), differed between island and mainland lizards. Geometric morphometric analyses revealed substantial differences between populations (Fig. 4). Island populations had a more elongated and less flattened head, but a similar HW relative to mainland lizards. An increase in head depth and width is related to higher bite force (McBrayer, 2004). Hence islanders, by increasing their head depth, should be able to achieve higher bite force than the mainland individuals.

Higher bite force in males was in accordance with our predictions as stronger bites are beneficial in the context of intraspecific agonistic encounters and, potentially, mating (Herrel *et al.*, 1999; Kwiatkowski & Sullivan, 2002; Lappin *et al.*, 2006; Moreira, López & Martín, 2006). Yet, these elements are not of the same significance to females, as females do not defend territories. Nonetheless, a difference between insular and mainland populations was expected because of its potential impact on feeding ecology. According to our findings, insular lizards have adopted a wider diet (wider H') that includes more plant material (Fig. 7). The consumption of plant material has been associated with higher bite force (Herrel *et al.*, 1999, 2001b). Herrel, Aerts & De Vree (1998) suggested that herbivory is correlated with a robust head and higher bite force. Moreover, an increase in bite force may considerably reduce prey handling time and increase prey processing efficiency (Verwajen *et al.*, 2002), which is important in low food abundance environments, such as islands. In addition, it has been proposed that lizards with wider dietary niche breadth exert higher bite forces, whereas low niche breadth values may eventuate in lower biting capacities (Edwards *et al.*, 2013). The aforementioned would be fully concordant with our results; however, female lizards do not appear to comply with this model.

We believe that this discrepancy can be explained by the fact that our study focused only on a few of the parameters related to bite force, such as head shape and size. We did not examine other important features, such as insertion angles, physiological properties of jaw muscles and the structure of the jaw muscle lever system (Herrel *et al.*, 2002; Schaerlaeken *et al.*, 2012). The detailed analysis of

the full array of the characters that are involved in bite force could shed light on the observed differences in males versus females.

In conclusion, bite force and head size and shape seem to be ecologically relevant variables that are probably subjected to natural and sexual selection in *L. trilineata*. However, our results fell short of the absolute proof of the effect of insularity on feeding apparatus morphology and performance. Although green lizards adapted their dietary habits and, at least partially, head morphology to the particular conditions of islands, bite force was affected only in the case of males. To entirely unravel how insularity affects bite force and head morphometrics, more studies including additional species and larger sample sizes are required.

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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:

Figure S1. The sampling areas differed in vegetation type and cover.