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# Sex-specific differences in ecomorphological relationships in lizards of the genus *Gallotia*

**Marta Lopez-Darias[1,2], Bieke Vanhooydonck[3], Raphael Cornette[4] and Anthony Herrel*[,5,6]**

[1]*Instituto de Productos Naturales y Agrobiología (IPNA), Consejo Superior de Investigaciones Científicas (CSIC), C/ Astrofísico Francisco Sánchez, 3 – 38206, Tenerife, Islas Canarias, Spain;* [2]*Instituto Mediterráneo de Estudios Avanzados (IMEDEA), Consejo Superior de Investigaciones Científicas (CSIC), C/ Miquel Marquès, 21 – 07190, Esporles, Balearic Islands, Spain;* [3]*Department of Biology, University of Antwerp, Universiteitsplein 1, B-2610 Antwerpen, Belgium;* [4]*UMR CNRS/MNHN 7205, 'Origine, Structure et Evolution de la Biodiversité', Muséum National d'Histoire Naturelle, 45 Rue Buffon, Paris 75005 France;* [5]*Département d'Ecologie et de Gestion de la Biodiversité, UMR 7179 C.N.R.S/M.N.H.N., 55 rue Buffon, Case Postale 55, 75005 Paris Cedex 5, France; and* [6]*Ghent University, Evolutionary Morphology of Vertebrates, K.L. Ledeganckstraat 35, B-9000 Gent, Belgium*

## Summary

**1.** Males and females often differ from one another in phenotypic traits due to differential investment in traits relevant to the fitness of each sex. However, how differences in sexually dimorphic traits affect ecologically relevant performance traits and whether these are correlated with variation in ecology remains poorly understood.

**2.** Here, we test the co-evolution of head shape, bite force capacity and diet in male and female lizards (*Gallotia*) from the Canary Islands, known to be sexually dimorphic. We collected data on bite force and head size and shape for both sexes of all seven extant species on all seven islands of the archipelago (ten evolutionary-independent lineages). Moreover, we collected diet data for five out of the seven species (eight lineages).

**3.** Our results show that the evolution of head morphology is associated with the evolution of bite force in both sexes. However, only in females is the evolution of head morphology and bite force associated with the evolution of diet. In males, head morphology and bite force are decoupled from the evolution of diet. In conjunction with the male head shape characterized by a broad rostrum, this suggests that head shape and bite force may be evolving principally under sexual selection in males.

**4.** Our data thus suggest that head morphology and associated functional traits may evolve under different selective pressures in the two sexes.

**Key-words:** bite force, diet, head shape, Lacertidae, lizard

## Introduction

Differences in phenotypic traits between the sexes have been the subject of intensive research since Darwin's seminal publication on 'The descent of man and selection in relation to sex' (1871). Differences between males and females of the same species can be many fold and may range from differences in overall body size (e.g. Shine 1989; Anderson & Vitt 1990; Butler 2007), over differences in colour pattern (Maynard-Smith & Harper 2003; Stuart-Fox & Ord 2004), to more subtle differences in head or limb dimensions (Lappin & Swinney 1999; Perry *et al.* 2004; Bruner *et al.* 2005; Herrel, McBrayer & Larson 2007; Kaliantzopoulou, Carretero & Llorente 2008). The selective pressures underlying phenotypic divergence between the sexes can be divided into two main, non-mutually exclusive categories: sexual selection and natural selection. Whereas sexually selected traits evolve because they confer a mating or reproductive advantage (Husak *et al.* 2006; Husak, Lappin & Van Den Bussche 2009), naturally selected traits may evolve because they result in reduced intersexual competition for scarce resources (Selander 1966; Schoener 1967; Vincent & Herrel 2007).

The general consensus in most cases is that both sexual and natural selection may play a role in establishing phenotypic differences between the sexes (Andersson 1994; Vincent & Herrel 2007). Yet, whether the phenotype is driven by similar selective pressures in both sexes remains poorly understood. In some lizards (*Liolaemus*), it has been suggested that the selective pressures acting upon the

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*Correspondence author. E-mail: anthony.herrel@mnhn.fr

two sexes may differ, with male morphology being principally driven by sexual selection through male–male competition, and female morphology being driven by natural selection (Vanhooydonck *et al*. 2010). This was suggested to be related to the inclusion of plant matter into the diet. As the consumption of plant matter requires large bite forces (Herrel, Van Damme & De Vree 1996; Herrel, Vanhooydonck & Van Damme 2004; Herrel *et al*. 2008), it was suggested that females, being the smaller sex, may evolve larger and differently shaped heads as high bite forces to allow them access to otherwise unavailable resources (i.e. plants). However, whether this is a more general pattern for lizards including plant matter into the diet, or restricted to relatively small-bodied *Liolaemus* lizards (Espinoza, Wiens & Tracy 2004), remains unknown.

Here, we use *Gallotia* lizards from the Canary Islands as a model to test for the evolutionary relationships between head morphology, bite force and diet in the two sexes. *Gallotia* is of interest as species in this genus have evolved large body size and a diet containing significant amounts of plant matter, similar to what has been observed in *Liolaemus* lizards (i.e. essentially becoming herbivorous; see Carretero *et al*. 2006; Cox, Carranza & Brown 2010). The inclusion of plant matter in the diet has been suggested to be related to the evolution of large body size, high bite forces, and large head size in both lacertid lizards (Herrel *et al*. 1999, 2004, 2008; Van Damme 1999) and lizards in general (Herrel, Vanhooydonck & Van Damme 2004; Herrel 2007). Indeed, plant matter is tough and forces needed to reduce even seemingly innocuous items such as leaves and flowers require large bite forces, often much higher than those required to crush most arthropods or small vertebrates (Herrel *et al*. 1999).

If the sexual dimorphism in head size in *Gallotia* is caused by divergent selective regimes in males and females (as has been suggested for *Liolaemus* lizards), then the evolution of head morphology in females should be correlated with the evolution of both bite force and diet. Given that females are the smaller sex, selection on bite force may be great to allow them to gain access to plants as a dietary resource. Conversely, in males, the evolution of head morphology and bite force may be decoupled from the evolution of diet if sexual selection is the principal driver of variation in head morphology. Indeed, many studies have shown that bite force in male lizards is related to male–male combat (Huyghe *et al*. 2005; Husak, Lappin & Van Den Bussche 2009) and generally much higher than those needed to reduce the average food item (Herrel *et al*. 1999, 2006; Herrel, McBrayer & Larson 2007). Moreover, we predict that intrasexual selection in males will select for head shapes allowing them to engage in male–male combat and defend territories (Lappin & Husak 2005), or alternatively to hold on to females during copulation (Herrel, Van Damme & De Vree 1996). In females, other shapes may be selected for and may allow them to optimize their ability to consume plant matter.

To explore differences in head shape, we use geometric morphometric analyses in addition to analyses of linear dimensions, allowing us to detect more subtle differences in morphology between the sexes. We further explore whether variation in head morphology is related to variation in bite force and diet to test for differences between sexes in these relationships. We predict based on data for *Liolaemus* lizards that in females head shape and bite force co-evolve with diet. For males, we predict that the evolution of head shape is associated with the evolution of bite force given its importance in male–male combat, but that neither head shape nor bite force co-evolve with diet.

## Materials and methods

The lacertid lizards from the Canary Islands belong to the endemic genus *Gallotia*. Seven extant species are recognized within the genus, each comprising several subspecies and inhabiting the main islands in the archipelago, as well as almost all the offshore small islets and rocks. The extant *Gallotia* species fall into two distinct size groups. A first group of small to medium-sized lizards [snout-vent length (SVL) 45–140 mm] is formed by *Gallotia atlantica*, present on the eastern islands of Lanzarote and Fuerteventura, *Gallotia galloti*, inhabiting Tenerife and La Palma, and by *Gallotia caesaris*, on La Gomera and El Hierro. A second group of ‘giant’ lizards (SVL 70–345 mm) is formed by *Gallotia stehlini*, an abundant species found throughout the island of Gran Canaria, and by the Critically Endangered (IUCN red list of threatened species, http://www.iucnredlist.org/) *Gallotia intermedia*, *Gallotia bravoana* and *Gallotia simonyi* that survive in limited numbers on isolated cliffs on the islands of Tenerife, La Gomera and El Hierro, respectively. Here, we exclude the giant species from La Palma, *Gallotia auaritae*, as its recent rediscovery remains controversial and there is no clear evidence to prove its presence on the island.

### LIZARD SAMPLING

During September 2011, we captured 451 specimens representing populations from the seven main islands of the Canary Islands and from all extant species in the genus *Gallotia* (Table 1). Specimens were captured in the wild by noose or using traps baited with tomatoes. Due to the conservation status of *G. bravoana* and *G. simonyi*, and because individuals exist in captivity in their respective recovery centers, specimens of these two species were measured at these facilities. Consequently, these species are not included in the diet analyses. All permissions required for capturing and manipulating *Gallotia* species were provided by each island Council and the Government of the Canary Islands. All animals captured in the field were measured and released within 24 h of capture.

### MORPHOMETRICS

Seven morphological measurements were taken using digital callipers (Mitutoyo, ±0·01 mm) for a total of 451 individuals. For each animal, we measured SVL, head length, head width, head depth and the lower jaw length from the back of the retroarticular process to the tip of the jaw (Herrel *et al*. 1999). All individuals were weighed to the nearest 0·5 g using a Pesola balance. We determined sex of each individual by checking for the presence of hemipenes. Of the entire sample, only adults (determined by the smallest body size where hemipenes could be easily everted in

**Table 1.** Summary of the biometric data collected for the species in this study (only adults are included)

| Species | Island | Sex (*N*) | SVL (mm) | Mass (g) | Head length (mm) | Head width (mm) | Head height (mm) | Lower jaw length (mm) | Bite force (*N*) |
|---|---|---|---|---|---|---|---|---|---|
| *Gallotia atlantica* | Fuerteventura | M (17) | 71·3 ± 5·3 | 9·2 ± 2·5 | 16·7 ± 1·2 | 10·1 ± 1·0 | 7·2 ± 0·7 | 18·4 ± 1·3 | 21·6 ± 7·9 |
| | | F (20) | 57·9 ± 4·0 | 4·2 ± 0·9 | 12·7 ± 0·8 | 7·2 ± 0·4 | 5·2 ± 0·4 | 13·4 ± 0·8 | 5·3 ± 1·5 |
| | Lanzarote | M (20) | 91·1 ± 6·0 | 21·0 ± 5·9 | 21·4 ± 1·5 | 14·0 ± 1·3 | 9·7 ± 1·2 | 23·9 ± 1·7 | 29·7 ± 5·9 |
| | | F (18) | 63·4 ± 5·9 | 7·8 ± 5·4 | 14·5 ± 1·5 | 8·3 ± 1·1 | 6·0 ± 0·8 | 15·5 ± 1·7 | 8·4 ± 3·6 |
| *Gallotia bravoana* | La Gomera | M (14) | 184·5 ± 7·2 | 210·5 ± 21·7 | 46·1 ± 1·9 | 31·6 ± 1·3 | 23·4 ± 1·4 | 48·2 ± 2·2 | 133·3 ± 10·7 |
| | | F (15) | 172·3 ± 5·8 | 159·2 ± 12·9 | 38·3 ± 1·5 | 26·2 ± 1·2 | 19·8 ± 0·7 | 40·1 ± 1·7 | 104·4 ± 9·2 |
| *Gallotia caesaris* | El Hierro | M (10) | 87·8 ± 5·1 | 18·5 ± 3·0 | 22·2 ± 1·2 | 12·8 ± 1·2 | 10·3 ± 0·9 | 24·1 ± 1·4 | 30·5 ± 8·6 |
| | | F (21) | 73·1 ± 5·7 | 9·3 ± 2·0 | 17·4 ± 1·0 | 9·6 ± 0·7 | 7·7 ± 0·6 | 18·5 ± 1·2 | 13·0 ± 2·8 |
| | La Gomera | M (7) | 96·9 ± 8·8 | 27·6 ± 7·7 | 24·9 ± 2·8 | 14·9 ± 3·0 | 11·9 ± 1·8 | 27·0 ± 12·8 | 40·1 ± 14·7 |
| | | F (20) | 84·6 ± 5·6 | 14·8 ± 3·0 | 19·3 ± 1·3 | 10·9 ± 0·9 | 8·6 ± 0·7 | 20·8 ± 1·5 | 15·9 ± 3·8 |
| *Gallotia galloti* | La Palma | M (14) | 113·4 ± 3·8 | 52·4 ± 3·6 | 28·6 ± 2·3 | 18·9 ± 0·6 | 14·7 ± 0·4 | 31·2 ± 2·4 | 79·5 ± 8·6 |
| | | F (22) | 91·8 ± 5·5 | 21·3 ± 5·0 | 21·1 ± 1·3 | 12·4 ± 0·9 | 9·9 ± 0·8 | 22·9 ± 1·5 | 26·3 ± 7·9 |
| | Tenerife | M (11) | 108·8 ± 3·7 | 38·9 ± 5·8 | 26·7 ± 2·2 | 17·6 ± 1·0 | 13·1 ± 0·8 | 29·8 ± 1·5 | 60·6 ± 7·8 |
| | | F (10) | 85·8 ± 8·0 | 18·4 ± 6·2 | 20·3 ± 2·1 | 11·8 ± 1·5 | 8·8 ± 1·3 | 21·7 ± 2·3 | 21·1 ± 11·1 |
| *Gallotia intermedia* | Tenerife | M (1) | 154·8 | 123·0 | 42·3 | 28·4 | 20·3 | 34·6 | 121·9 |
| | | F (4) | 122·2 ± 18·2 | 59·7 ± 33·3 | 28·3 ± 3·6 | 17·9 ± 1·7 | 13·4 ± 1·8 | 30·3 ± 3·5 | 48·0 ± 21·3 |
| *Gallotia simonyi* | El Hierro | M (11) | 236·5 ± 11·3 | 446·2 ± 81·1 | 56·8 ± 3·2 | 40·7 ± 3·1 | 30·3 ± 2·5 | 61·1 ± 3·6 | 143·0 ± 23·3 |
| | | F (14) | 196·1 ± 8·6 | 238·6 ± 32·9 | 42·6 ± 2·3 | 28·3 ± 3·2 | 22·1 ± 0·9 | 45·0 ± 2·8 | 105·6 ± 9·0 |
| *Gallotia stehlini* | Gran Canaria | M (16) | 189·1 ± 22·5 | 235·4 ± 99·3 | 48·2 ± 7·9 | 32·2 ± 5·6 | 24·3 ± 5·0 | 51·6 ± 7·8 | 124·1 ± 23·6 |
| | | F (25) | 156·8 ± 14·9 | 107·6 ± 28·1 | 35·6 ± 4·3 | 22·4 ± 3·0 | 17·1 ± 2·2 | 38·2 ± 4·5 | 83·7 ± 14·0 |

M, male; F, female; SVL, snout-vent length.

males and where eggs could be detected by palpation in females) were retained for analyses resulting in a total of 281 specimens (see Table 1 for sample sizes).

Dorsal head shape was quantified using landmark-based geometric morphometric methods (Rohlf 1993, 1995; Rohlf & Marcus 1993). High-resolution photographs (in dorsal and lateral view) of all individuals were taken with a digital camera (Nikon D70). Photographs were made with a grid as a background for scaling, and lizards were held such that the head was parallel to the grid paper. Images where lizards were not properly aligned or where landmarks were not visible were discarded from the analysis. This resulted in a total of 245 individuals that could be retained for our analysis. A preliminary analysis of the pictures taken of the head in lateral view indicated that this view was uninformative relative to variation in bite force (i.e. no correlations between head shape in lateral view and bite force were observed) and these pictures were thus not used for subsequent analyses. Note, however, that head dimensions such as height were included in the analysis.

On each image in dorsal view, 15 landmarks and 50 sliding semilandmarks (Bookstein 1997) on each side of the head were recorded using TpsDig (Rohlf 2001; Fig. 1). Landmarks were chosen based on their reliability of identification in all specimens, in addition to their coverage of regions that could be functionally important. Whereas our anatomical landmarks capture shape differences in the rostrum, our sliding landmarks outline the upper temporal bar, an important attachment site for the principal jaw adductors (m. adductor mandibulae externus group; Fig. 1). The sliding step was performed using TpsDigRelw (Rohlf 2010) while minimizing Procrustes distances as this method gives slightly better results in term of shape discrimination (Sheets *et al.* 2006). Next, generalized Procrustes analyses (GPA) were performed (Rohlf & Slice 1990) followed by a principal component analysis (PCA). For all analyses, GPA and PCA were conducted on data for both sexes separately to test whether principal axes of variation in head shape within each sex were related to bite force and diet. All morphometric analyses and shape visualizations were performed in R (R Development Core Team, 2013) using the RMORPH package (Baylac 2012).

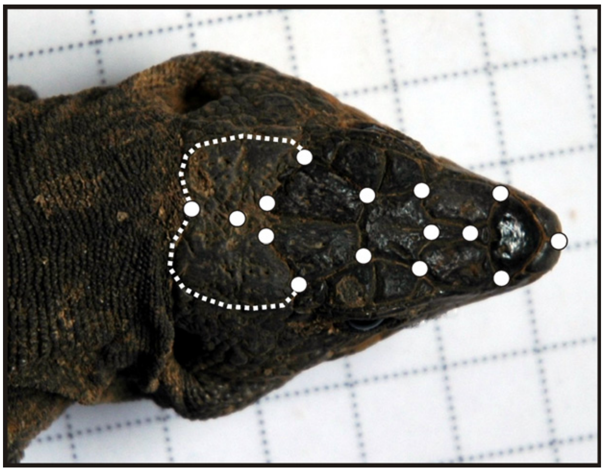

**Fig. 1.** Dorsal view of a *Gallotia atlantica* lizard showing the landmarks (circles) and semilandmarks on curves (dashed line) used in the geometric morphometric analysis.

### BITE FORCE

We measured *in vivo* bite forces for all individuals using an isometric Kistler force transducer (type 9203, range ±500 N; Kistler Inc., Winterthur, Switzerland) connected to a portable Kistler charge amplifier (type 5995A; Kistler Inc.; see Herrel *et al.* 1999 for a detailed description of the set-up). Measurements were repeated five times for each animal, and the maximum value obtained during such recording sessions was considered to be the maximal bite force for that animal.

### DIET ANALYSIS

Diet was quantified by stomach flushing (Herrel *et al.* 2006). Animals were stomach-flushed directly after capture using a syringe with a ball-tipped steel needle attached. The size of the syringe and needle was adjusted to the size of the animal. Animals were tapped gently on the sides of the jaw, resulting in a threat response, in which the jaws are opened widely. A small plastic ring was inserted between the jaws to allow unhindered flow of water and food out of the digestive tract. The needle was gently inserted into the pharynx and pushed further down the digestive tract to the end of the stomach (the position of the needle could be detected by palpation). Next, water was gently squeezed out of the syringe while massaging the stomach of the lizard. Water was added until the food was regurgitated or pushed out with the water. Stomach contents were stored in labelled vials in a 70% aqueous ethanol solution. In the laboratory, all prey items were identified to order (Table 2) using a stereomicroscope (6–10× magnification). Plant and animal material was weighed separately, and the vegetable content was in turn divided into five categories: flowers, fruit/seeds, leaves, stems and other plant debris. Tomato retrieved from the stomachs was not included into the analyses as traps were baited with tomato. Both the fleshy parts of the tomato and its seeds could be easily identified in the stomachs as traps were checked every 30 min. All different items extracted from each stomach content remained in an oven (J.P. Selecta, Inc., Abrera, Barcelona, Spain) at 50 °C for 15 h to dehydrate them fully and were then weighed using a precision balance (to the nearest 0·0001 g; Mettler Toledo, Inc., Viroflay, France) to quantify the importance of each type of prey in the diet according to its biomass.

### STATISTICAL ANALYSES

We considered populations of the same species on a different island as a distinct evolutionary unit (Fig. 2) and thus treated them as different in the analyses. Morphological and bite force data were $\log_{10}$-transformed, and the proportions of different food items into the diet were arcsine-transformed before analyses. Means per sex and species on an island were calculated and used for the independent contrast analyses.

To test for the co-evolution between the proportion of plant matter in the diet, head dimensions (length, width, height and lower jaw length), head shape (the first three shape axes extracted from the geometric morphometric analysis performed for each sex separately, together explaining 70% of the variation) and bite force, we calculated the independent contrasts of the population (island) means for each species. We used the PDAP package (Garland *et al.* 1993) implemented in Mesquite (Maddison & Maddison 2011, http://www.mesquiteproject.org) to calculate the independent contrasts. The phylogeny was based on molecular studies of the genus and includes divergence dates for the different lineages (Cox, Carranza & Brown 2010). We used the diagnostics implemented in PDAP to check whether branch lengths derived from the molecular study were indeed appropriate, which was the case. Analyses were run for males and females separately as *Gallotia* are known to be dimorphic (Herrel *et al.* 1999; Molina-Borja 2003; Molina-Borja & Rodríguez-Domínguez 2004; Molina-Borja *et al.* 2010). Co-evolution between traits (head dimensions, head shape, bite force and diet) was tested by running bivariate regressions between the independent contrasts forced through the origin. As the different traits are known to co-vary with size in lizards (see Herrel & O'Reilly 2006; Herrel *et al.* 2004, 2006), we first extracted residuals from regressions of all traits on body size (forced through the origin). Next, we regressed residual contrasts of morphology (i.e. the first three shape axes, head length, head width, head height and lower jaw length) on the residual contrasts

**Table 2.** Diet of the different species of adult *Gallotia* sampled in this study.

| | | | % Animal matter (dried weight) | | % Vegetal matter (dried weight) | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Sample size | | Total | | Total | | % Fruits | | % Flowers | | % Leaves | | % Stems | | % Other | |
| Sex | Male | Female | Male | Female | Male | Female | Male | Female | Male | Female | Male | Female | Male | Female | Male | Female |
| *Gallotia atlantica* | | | | | | | | | | | | | | | | |
| Fuerteventura | 17 | 20 | 26·1 | 21·7 | 73·9 | 78·3 | 0·7 | 5·8 | 50·3 | 63·7 | 0·0 | 0·0 | 0·7 | 0·0 | 22·2 | 8·8 |
| Lanzarote | 20 | 18 | 4·2 | 38·7 | 95·8 | 61·3 | 68·4 | 13·4 | 9·3 | 31·2 | 0·0 | 0·0 | 0·0 | 0·0 | 18·2 | 16·7 |
| *Gallotia caesaris* | | | | | | | | | | | | | | | | |
| El Hierro | 10 | 21 | 14·8 | 30·5 | 85·2 | 53·7 | 14·3 | 13·2 | 14·3 | 8·0 | 0·0 | 3·6 | 0·0 | 1·3 | 56·6 | 27·5 |
| La Gomera | 7 | 19 | 15·2 | 11·4 | 64·8 | 79·5 | 0·0 | 22·6 | 31·8 | 30·9 | 0·0 | 7·3 | 0·0 | 0·0 | 33·0 | 18·7 |
| *Gallotia galloti* | | | | | | | | | | | | | | | | |
| La Palma | 14 | 22 | 2·8 | 15·3 | 97·2 | 84·7 | 18·5 | 11·8 | 20·0 | 10·4 | 0·0 | 22·6 | 0·0 | 1·6 | 58·7 | 38·2 |
| Tenerife | 11 | 10 | 0·0 | 20·3 | 100·0 | 79·7 | 24·2 | 79·7 | 26·6 | 0·0 | 0·0 | 0·0 | 0·0 | 0·0 | 49·3 | 0·0 |
| *Gallotia intermedia* | | | | | | | | | | | | | | | | |
| Tenerife | 0 | 4 | – | 0·0 | – | 100·0 | – | 92·8 | – | 0·0 | – | 7·2 | – | 0·0 | – | 0·0 |
| *Gallotia stehlini* | | | | | | | | | | | | | | | | |
| Gran Canaria | 16 | 25 | 1·3 | 5·9 | 98·7 | 94·1 | 19·7 | 9·6 | 14·5 | 28·5 | 7·6 | 12·1 | 10·7 | 8·0 | 46·2 | 36·0 |

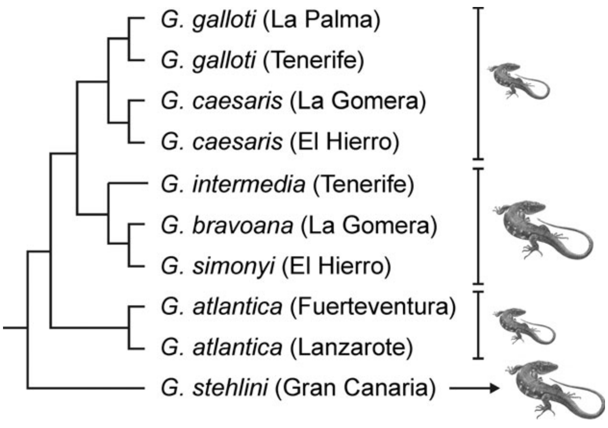

**Fig. 2.** Phylogenetic relationships of the different species and populations on the different islands used in our analyses. To the right is illustrated whether the species are large or of small body size. The relationships are based on Cox, Carranza & Brown (2010). Although the divergence times between populations provided in Cox, Carranza & Brown (2010) were incorporated into the analyses, the branches on the figure are not drawn proportional to time.

of bite force (Table 3). Finally, we regressed the residual contrasts of morphology (the first three shape axes, head length, head width, head height and lower jaw length) and bite force on the proportion of plant matter in the diet (Table 3).

As diet data were not available for all species and individuals, we ran separate analyses when testing relationships between morphology and diet vs. those testing relationships between bite force and head shape only. The phylogeny was adjusted by pruning taxa where needed. All analyses on the independent contrasts were conducted using IBM SPSS statistics (V. 20, Armonk, NY, USA).

## Results

A principal component analyses of head shape in males resulted in three axes that jointly explained 69·5% of the overall variation in the data set. The first axis (42%) contrasts animals with short and narrow rostra and wide adductor chambers on the positive side of the axis with animals with long and wide rostra yet narrow and slightly more elongated adductor chambers (Fig. 3). The second axis (18·5%) contrasts animals with shorter rostra and slightly longer adductor chambers with animals with longer rostra and shorter adductor chambers on the negative side of the axis (Fig. 3). The third axis (9%) contrasts animals with narrow rostra and rounder adductor chambers on the positive side with animals with wider rostra and more squarer adductor chambers on the negative side of the axis (Fig. 3). In females, the first three axes explained 72·2% of the overall variance in the data set. The first axis (47·6%) contrasts animals with short and narrow rostra and wide adductor chambers on the positive side of the axis to animals with long and wide rostra yet narrow and slightly more elongated adductor chambers similar to what was observed in males (Fig. 3). The second axis (16·2%) contrasts animals with long rostra and short adductor chambers on the positive side of the axis to animals with short rostra and longer adductor chambers on the negative side of the axis, a pattern that is the inverse of the one observed for males (Fig. 3). The third axis (8·4%) contrasts animals with wider rostra and posteriorly slightly wider adductor chambers on the positive side of the axis to animals with narrower rostra and anteriorly slightly wider adductor chambers on the negative side (Fig. 3).

In males, external head dimensions (length, width and depth) co-evolve with bite force (i.e. using residual-independent contrast data; see Table 3). The evolution of a relatively high bite force in males was associated with the evolution of head shape axis two only (Fig. 4). This suggests that the evolution of a high bite force is associated with the evolution of robust and short rostra and slightly longer adductor chambers (Fig. 3). The evolution of high bite force independent of body size was associated with the evolution of relative head dimensions in females as well (head width and depth; see Table 3). The evolution of residual bite force in females was also associated with the evolution of head shape as described by the first two shape axes. This indicates that the evolution of high bite force in females is associated with the evolution of short narrow rostra and wide and long adductor chambers (Fig. 3).

In males, the proportion of plant matter in the diet was associated with neither the evolution of head morphology nor the evolution of bite force (all $P > 0{\cdot}05$; Table 3), indicating that the evolution of diet is decoupled from the evolution of both head morphology and bite force. In females, the evolution of a larger proportion of plants in the diet independent of body size was associated with the evolution of a relatively shorter lower jaw length and head length (Table 3). Moreover, head shape axis two was associated with the evolution of a larger proportion of plant matter into the diet (Fig. 4, Table 3), indicating that the evolution of females with longer adductor chambers and shorter rostra is associated with the evolution of a more herbivorous diet. The evolution of a larger proportion of plant matter into the diet was also associated with the evolution of bite force (Table 3).

## Discussion

In males, the evolution of head morphology was associated to the evolution of bite force but not diet; in females, the evolution of head morphology was associated with the evolution of both bite force and diet, suggesting differences in the evolutionary pressures driving the evolution of head shape in both sexes. As predicted, different traits co-evolved with bite force in the two sexes. These results are similar to what has been observed for South American *Liolaemus* lizards where in males the evolution in bite force was not associated with the evolution of diet and was predicted by other morphological traits than in females (Vanhooydonck *et al.* 2010). This suggests that head dimensions and bite force in male and female lizards may be under different selective pressures with female head shape being driven at least partially by natural selection and diet.

**Table 3.** Results of the independent contrast analyses

| | | *r* | *P* |
|---|---|---|---|
| Males | | | |
| Residual shape axis 1 | Residual bite force (*N*) | 0·52 | 0·12 |
| **Residual shape axis 2** | **Residual bite force (*N*)** | **0·88** | **0·001** |
| Residual shape axis 3 | Residual bite force (*N*) | 0·15 | 0·68 |
| **Residual head length (mm)** | **Residual bite force (*N*)** | **0·74** | **0·02** |
| **Residual head width (mm)** | **Residual bite force (*N*)** | **0·84** | **0·002** |
| **Residual head depth (mm)** | **Residual bite force (*N*)** | **0·78** | **0·008** |
| Residual lower jaw length (mm) | Residual bite force (*N*) | 0·26 | 0·47 |
| Residual shape axis 1 | Residual proportion of plants | 0·17 | 0·69 |
| Residual shape axis 2 | Residual proportion of plants | 0·52 | 0·19 |
| Residual shape axis 3 | Residual proportion of plants | 0·49 | 0·22 |
| Residual head length (mm) | Residual proportion of plants | 0·55 | 0·16 |
| Residual head width (mm) | Residual proportion of plants | 0·06 | 0·90 |
| Residual head depth (mm) | Residual proportion of plants | 0·47 | 0·24 |
| Residual lower jaw length (mm) | Residual proportion of plants | 0·13 | 0·76 |
| Residual bite force (*N*) | Residual proportion of plants | 0·44 | 0·27 |
| Females | | | |
| **Residual shape axis 1** | **Residual bite force (*N*)** | **0·77** | **0·009** |
| **Residual shape axis 2** | **Residual bite force (*N*)** | **−0·57** | **0·088** |
| Residual shape axis 3 | Residual bite force (*N*) | 0·28 | 0·43 |
| Residual head length (mm) | Residual bite force (*N*) | 0·56 | 0·093 |
| **Residual head width (mm)** | **Residual bite force (*N*)** | **0·77** | **0·009** |
| **Residual head depth (mm)** | **Residual bite force (*N*)** | **0·87** | **0·001** |
| Residual lower jaw length (mm) | Residual bite force (*N*) | 0·52 | 0·12 |
| Residual shape axis 1 | Residual proportion of plants | 0·42 | 0·3 |
| **Residual shape axis 2** | **Residual proportion of plants** | **−0·73** | **0·04** |
| Residual shape axis 3 | Residual proportion of plants | 0·06 | 0·89 |
| **Residual head length (mm)** | **Residual proportion of plants** | **−0·82** | **0·013** |
| Residual head width (mm) | Residual proportion of plants | 0·64 | 0·086 |
| Residual head depth (mm) | Residual proportion of plants | 0·68 | 0·06 |
| **Residual lower jaw length (mm)** | **Residual proportion of plants** | **−0·88** | **0·004** |
| **Residual bite force (*N*)** | **Residual proportion of plants** | **0·73** | **0·038** |

Note that $N = 9$ for analysis with residual bite force; $N = 7$ for analyses with the residual proportion of plant matter into the diet. Bolded rows indicate significant results. All regressions were forced through the origin.

Head shape in males, in contrast, appears to evolve under sexual selection pressures. Note that we only examined relationships between bite force and the proportion of plant matter in the diet and thus other aspects of the diet not examined here could potentially exert additional selective pressures on head shape in male. The evolution of high bite force under a sexual selection scenario could allow males to incorporate a larger amount of plant matter into the diet as well. This is observed in our data set where adult males often eat more plant material than females (Table 2). Interestingly enough, however, females include more tough plant items such as leaves and stems into their diet, while males eat more fruits and flowers on average (Table 2). The fact that in males the evolution of high bite force is associated with the evolution of a short and robust rostrum suggests that this may be a consequence of selection through male–male combat (Fig. 3). In many lizards, including *Gallotia*, males will bite each other and head-lock during territorial fights (A. Herrel & M. Lopez-Darias, pers. obs.). During such head locking, animals vigorously turn about their long axes imposing significant torsional strain on the jaws. Having short and robust rostra may thus be beneficial in preventing mechanical failure and injury during such interactions. Additionally, robust rostra may also be beneficial for holding on to females during copulation.

Of the external head dimensions examined, head width was the best predictor of bite force in males as was previously demonstrated for the species *G. galloti*. As head width has been shown to be important in determining the outcome of male–male contests in *Gallotia* (Molina-Borja, Padron-Fumero & Alfonso-Martin 1998; Huyghe *et al.* 2005), this further supports the idea that head shape in males evolves principally through sexual selection. Despite these patterns, it must be noted that the evidence provided here is correlational only, and thus, explicit tests of these hypotheses are needed. Moreover, future studies investigating this pattern in other lizards would be especially insightful in determining the generality of this phenomenon.

The factors that are associated with bite force evolution in the clade varied in interesting ways between males and females. In females, the evolution of relatively high bite force (i.e. independent of overall size variation) was associated with the evolution of taller heads, shorter snouts and

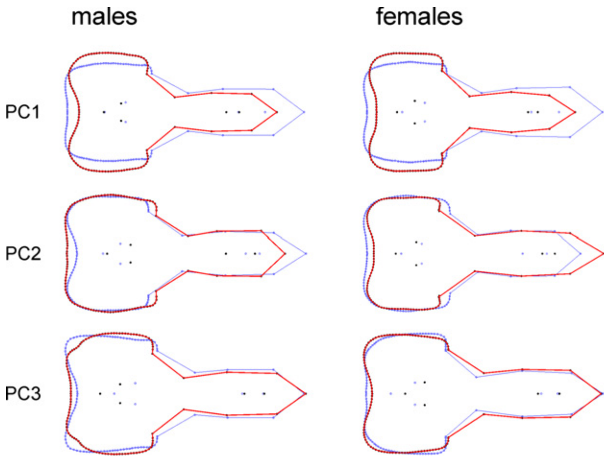

**Fig. 3.** Figure illustrating the head shapes associated with the first three principal components for males (left) and females (right). The red shapes represent shapes associated with the positive side of the axis, and blue shapes represent shapes associated with the negative side of the axis.

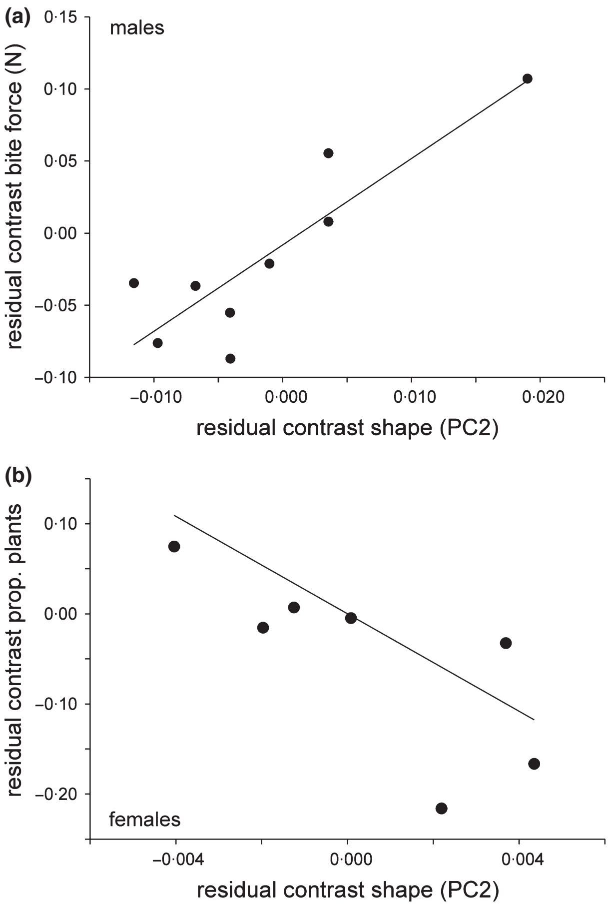

**Fig. 4.** Scatter plots illustrating (a) the co-evolution of head shape as described by principal component axis two and bite force independent of variation in overall body size in males and (b) the co-evolution of head shape as described by principal component axis two and the proportion of plant matter in the diet independent of variation in overall body size in females. Note that regressions are forced through the origin and that each species on an island was considered an independent evolutionary unit and thus data point. Thus, nine contrasts are presented in the figure.

larger adductor chambers all traits likely optimizing the reduction of tough and fibrous material like plants. In males, the evolution of bite force was associated with the evolution of overall head size and the evolution of shorter snouts and slightly longer adductor chambers. The giant species (both sexes) are, however, characterized by relatively long snouts and narrower adductor chambers suggesting that for their body size, they are not capable of generating very high bite forces. Thus, despite the strong co-evolution of diet with bite force and head shape in females, our results suggest that the largest species with the greatest absolute bite forces and the greatest proportion of plant matter in the diet do not necessarily possess the greatest relative bite force. This result, although at first sight counterintuitive, may be the result of the fact that large absolute bite forces (due to their large size) observed in these large species are sufficient to reduce all plant material encountered (see Herrel *et al.* 1999). Yet, for smaller species, the need to have relatively larger bite forces when including a larger proportion of plant matter into the diet is likely strong, and presumably drives the evolution of head shapes with short snouts and large adductor chambers. For example, female *G. atlantica* on Lanzarote consumed up 61% plant matter despite being the population with the smallest body size included in our study. However, their heads are characterized by short snouts and large adductor chambers, allowing them to generate relatively high bite forces. In comparison to other lizards (e.g. Herrel, De Grauw & Lemos-Espinal 2001; Herrel *et al.* 2001; Lappin, Hamilton & Sullivan 2006; Vanhooydonck *et al.* 2010), different traits co-evolved with bite force in *Gallotia* which is not surprising *per se*, as different variables were used in the analysis.

Whereas our data suggest that the evolution of head morphology in female, but not male, *Gallotia* is linked to the evolution of plant consumption, these results should be interpreted with some caution as we sampled diet only during one period of the year. It is known that diet in *Gallotia* can fluctuate seasonally (Valido, Nogales & Medina 2003; Rodriguez *et al.* 2008) and as such, our data may not be able to characterize the year-round diet in these species. Yet, given that our sampling took place in September when insect abundance is low and the proportion of plant matter in the diet is highest (Valido, Nogales & Medina 2003), we believe that our data represent the period when selection on bite force and head shape in relation to diet is likely highest. As such, our data may give a fairly accurate representation of whether the evolution of head morphology is driven by different selective pressures in the two sexes. Moreover, despite the relative small number of individuals included in our diet analysis for some populations, our results mimic those reported by other authors (Valido & Nogales 1994, 2003; Valido, Nogales & Medina 2003; Martin *et al.* 2005; Carretero *et al.* 2006). Our data show that the giant species *Gallotia intemedia* and *G. stehlini* nearly exclusively eat plant matter, supporting previously suggested relationship between body size and herbivory in lizards (Van Damme 1999; Valido & Nogales 2003; Herrel *et al.* 2004). Moreover, interesting island-level differences in diet and bite force were observed and mirror population level differences in morphology (Molina-Borja 2003), suggesting that populations on different islands may be diverging along different evolutionary trajectories.

In summary, our data demonstrate that in *Gallotia* lizards, the factors that drive the evolution of head morphology appear to be different for the two sexes, a pattern that merits to be explored further in other species.

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## Data accessibility

All data are presented in the article.

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