African Journal of Herpetology,
Vol. 65, No. 1, 2016, 1–20

Sexual dimorphism in morphological traits and scaling relationships in two populations of *Gallotia stehlini* (Fam. Lacertidae: Squamata) from Gran Canaria

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Abstract.—Lizards of the genus *Gallotia*, endemic to the Canary Islands, show morphological and colouration varieties that are related to within island variation in orographic and climatic characteristics. This study examines sexual size dimorphism (SSD) within and between population variation in morphological traits, and scaling relationships in *G. sthelini* from a southwestern locality (Tasartico) and from another (Gáldar) in the northwest of Gran Canaria. Both sites differ in climate and vegetation traits, and we hypothesised that SSD should be manifested by males having relatively larger body traits than females and that hind limb lengths should be relatively larger in individuals from the more open habitat. Results showed that one-third of the largest lizards from both populations did not differ significantly either in snout-to-vent length (SVL) nor in trunk length (TRL), but overall males had significantly larger SVL and TRL than females. Multivariate analysis showed that head width (HW) and hind limb length (HLL) were significantly larger in individuals from Tasartico than in those of Gáldar. Hind limb length was the trait that contributed most to differentiate between populations and head parameters between males and females. In both populations head and body traits scaled to TRL, head width (HW) and head depth (HD) of males having a positive allometry, and fore limb length (FLL) and hind limb length (HLL) a negative one. In relation to head length (HL), females had significantly larger TRL and smaller head depths than males; lizards from Gáldar had significantly larger trunk length (TRL), but smaller HW and HLL than those of Tasartico. We outline the multiple factors that could affect the evolution of morphometric traits of each sex, taking into account the ecological features of the two zones.

Key words.—Interpopulation differences; morphological traits; lizards; *Gallotia stehlini*.

INTRODUCTION

Variability within and between populations is common in morphological and behavioural traits of individuals from many taxa and its study is useful to uncover particularities of their adaptation and evolution (Emerson & Arnold 1989). Within reptiles, geographical variation in morphological, behavioural and/or life-history traits have been analysed, for

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ISSN 2156-4574 print/ISSN 2153-3660 online

http://dx.doi.org/10.1080/21564574.2015.1130755
http://www.tandfonline.com

example, in populations of *Zootoca vivipara* (Pilorge 1987), some species of *Gallotia* (Thorpe & Brown 1989), several *Anolis* species (Losos 1990a, 1990b), tree lizards (*Urosaurus ornatus,* Hews *et al*. 1997; Herrel *et al*. 2001), *Crotaphytus collaris* (McCoy *et al*. 1997) and several *Sceloporus* species (Sites *et al*. 1992). A frequent result of population and comparative analyses is the presence of sexual dimorphism that is manifested in males having larger snout-to-vent length (SVL) than females (sexual size dimorphism, SSD; Carothers 1981, 1984), the contrary (Fitch 1978) or no sexual dimorphism. The types of sexual dimorphism are currently interpreted as a result of different selective forces acting separately on each sex (Shine 1989; Andersson 1994; Fairbairn 1997; Kaliontzopoulou *et al.* 2015); for example, larger and stronger males are usually found in species in which male competition is an important factor in their reproductive success (Stamps 1983) and larger females in those species where an increase in female reproductive output has been selected (Shine 1989; Cooper & Vitt 1989). However, alternative hypotheses have also been considered (Schoener *et al.* 1982; Cooper & Vitt 1989; Shine 1989, 1991) including demographic causes (Stamps *et al.* 1997), natural selection acting differentially in both sexes (ecological niche segregation, Pérez-Mellado & de la Riva 1993) or phenotypic plasticity (Madsen & Shine 1993; Roitberg 2007). Sexual differences have also been analysed by scaling relationships of morphological traits, commonly with reference to SVL (Fairbairn 1997) but also in relation to trunk length (see Braña 1996; Scharf & Meiri 2013), showing that some traits such as head size or hind limb lengths are positively allometric in males while isometric or negatively allometric in females (Molina-Borja 2003; Kaliontzopoulou *et al.* 2007). These different sex-related scaling relationships have been proposed to result from both proximal and ultimate causes (Frynta *et al*. 2010; Pélabon *et al*. 2014) and also have proved to have ecological consequences (Vincent & Herrel 2007) that seem to be a by-product of sexual selection (at least in lacertid lizards, Herrel *et al*. 1999).

Such pressures vary between populations likely due to differences in habitat, climate and predation pressure (Kaliontzopoulou *et al.* 2010; Horváthová *et al.* 2013; Roitberg *et al*. 2015) and this could also be the case for lizards within Gran Canaria where dramatic climatological and habitat differences exist between north and south (Fernandopulle 1976). Lizard species belonging to *Gallotia*, a basal genus within lacertids, are endemic to the Canary Islands (Arnold 1973, 1989) and probably had ancestors from north Africa or southern Europe (Hipsley *et al*. 2009). Seven living species have been described and, given the monophyletic origin of this genus, comparative analysis of morphometric, ecological, behavioural and life history traits within and between populations may provide valuable information about local variability; this will help us to understand possible adaptations as well as evolutionary relationships. Given the variety of habitats occurring on a single island, opportunities exist for different selective factors to act on different populations within a species (e.g. Losos *et al.* 1997, for Caribbean *Anolis*).

Some species of *Gallotia* have been analysed from different taxonomic, ecological, morphological and behavioural points of view (Bischoff 1985, 1998; Thorpe & Brown 1989, 1991; Molina-Borja *et al.* 1997, 2010; Molina-Borja & Rodríguez-Domínguez 2004). *Gallotia stehlini* Schenkel 1901 is the sister taxon of all other species (Cox *et al.* 2010, and see Fig. 2 of Baeckens *et al.* 2015) and several publications have dealt with its description, body scalation, general biology, sprint speed (Thorpe & Báez 1993; Bannert 1998; Cejudo & Márquez 2001; Mateo 2002) and more recently with bite force, morphology and feeding in a comparative analysis (López-Darias *et al.* 2014).

This species has been considered the largest extant lizard of the genus (up to 260–280 mm maximum male SVL; Bischoff 1985; Mateo 2002). It inhabits Gran Canaria (a small introduced population is also present at Fuerteventura; Naranjo *et al.* 1992) and occupies different habitats within the island, from the seashore up to high altitudes (1950 m.a.s.l.). As with other *Gallotia* species, *G. stehlini* is mainly omnivorous, oviparous and reproduction occurs once a year during spring to summer (Bannert 1998; Carretero *et al*. 2006). There are within island contrasting differences in climate and vegetation, mainly between the northern and southern sectors, and thus morphological variation is expected to be influenced by local ecological factors. Though morphometric interpopulation analyses have been performed for other *Gallotia* (Thorpe & Báez 1987; Molina-Borja *et al.* 2010), no previous study has undertaken such an analysis for *G. stehlini*; however, Thorpe & Báez (1993) showed geographical variation of some scalation parameters across several populations, suggesting it was mainly due to adaptation to current ecological conditions. We selected two different habitats where *G. stehlini* is present and which have contrasted climates and vegetation to analyse morphological variation within each population, between populations and between sexes.

The specific objectives of the present paper are to analyse: (1) sexual dimorphism in SVL, trunk length (TRL) and several head and body traits from two populations of *G. stehlini* living in very different habitats; (2) scaling relationships (isometry or allometry) of different traits to SVL and TRL in both sexes from each population. We predicted that: (a) Males should have larger head sizes and hind limb lengths than females (a sexual dimorphism that occurs in other *Gallotia* species); moreover, according to previous findings in many lizards (Braña 1996; Scharf & Meiri 2013), females should have relatively larger trunk lengths and relatively smaller head lengths than males: (b) males should have steeper slopes (or higher elevation) in the relationships between morphometric traits to SVL or head length (HL) than females; and (c) as occurs in several other lizard species, hind limb lengths should be relatively larger in lizards from the more open habitat (where longer hind limbs could increase the probability of escaping from predators).

MATERIALS AND METHODS

Collecting Sites and Lizard Measurements

We selected two different habitats for collecting specimens, one in a ravine at Gáldar (90–120 m a.s.l., 28° 09′ 26″ N, 15° 40′ 01″ W) in the northwest of the island, and another one in a ravine at Tasartico (160–200 m a.s.l., 27° 55′ 12″ N, 15° 48′ 29″ W) from the southwest. Climate in the first habitat is warm and wet, and the vegetation is mainly composed of specimens of *Euphorbia balsamifera* (Fam. Euphorbiaceae), *Kleinia neriifolia* (Fam. Asteraceae) and *Opuntia dilenii* (Fam. Cactaceae). In the second habitat, hotter and drier than the first one, the main plants were *Plocama pendula* (Fam. Rubiaceae), *Launaea arborescens* (Fam. Asteraceae), *E. canariensis* (Fam. Euphorbiacae) and *Lycium* sp. Density of shrubs (as calculated from aerial photographs) was 0.14 and 0.034 per m^2, respectively, for the first and second habitats.

On each site, we put out traps to capture lizards one day per month, between April and July of 1996, 1998 and 1999. For the captures we used large plastic containers (50 cm high, 40 cm diameter) baited with pieces of tomato and banana. Lizard densities were not estimated but the number of captured lizards per sampling day was somewhat larger in Tasartico (8.75) than in Gáldar (8.2) population.

Immediately after capture, we measured SVL for each individual with a plastic ruler, and with a digital calliper (0.01 mm precision): head length (HL, distance between the snout and the rear border of occipital scale); head width (HW, distance between rear lateral edge of both parietal scales), head depth (HD, height between rear edge of parietal scale and lower border of the jaw), fore and hind limb lengths (FLL, HLL, distances between groin and distal end of longer finger from each limb) and trunk length (TRL) was calculated as the difference between SLV and HL. Body mass (BM) was taken by means of a spring scale (± 2 g precision). For bilateral traits, measurements were always done on the right.

Those lizards having a body size greater than the minimum size at sexual maturity were considered as adults: smallest male having easily evaginable hemipenes (SVL = 146.0 mm) and from the smallest female having enlarged ovarian follicles (SVL = 135.0 mm) (see Molina-Borja & Rodríguez-Domínguez 2004). Individuals with SVL smaller than 135 mm were considered as juveniles and due to their low number in each population they were included only for basic statistics but were not considered for sexual dimorphism and scaling calculations. Immediately after the measurements, all lizards were released unharmed at their capture site.

Data Analysis

Data were analysed using SPSS version 21.0 (IBM Corp., 2012), initially tested for assumptions of normality and homoscedasticity when applying parametric tests (MANCOVA and ANOVA analyses) and otherwise we applied a non-parametric test (PERMANOVA, see below).

Sexual dimorphism in body size.—SVL has not been considered an ideal measure of body size in lizards, as it reflects the evolutionary processes that may have been acting separately on both head size and trunk size (Kratochvil *et al*. 2003, Scharf & Meiri 2013). Moreover, considering that body growth after maturity is usually asymptotic in lizards and that mean SVL measurements do not allow robust comparison between groups because of the dependence on sample age structure (Stamps 1993; Brown *et al*. 1999), mean SVL (or TRL) is not an appropriate parameter for calculating sexual size dimorphism. Therefore, to quantify the differences in body length and to compare our results with that of other lizard species, we tested the differences in log-transformed SVL and TRL of the third largest individuals between sexes—excluding juveniles—within each population; as these data were not homoscedastic, we applied a PERMANOVA (Permutational Multivariate Analysis of Variance, within the statistical package Primer v 6; Clarke & Gorley 2006). In comparison to parametric tests, PERMANOVA does not require data to adhere to their strict conditions, and tests the simultaneous response of one or more variables to one or more factors in an ANOVA experimental design on the basis of any distance measure, using permutation methods (999 permutations, Anderson 2001).

Multivariate analysis of interpopulation and intersexual variation in body and head traits.—We performed comparisons between the two populations and sexes using body and head traits ($\log_{10}$ transformed). For this we used MANCOVA taking all $\log_{10}$ transformed data traits (except SVL) as dependent variables, site and sex as fixed factors, their interaction, and TRL as covariate. When a significant result was found, we also used univariate statistical analyses (ANOVAs with Sidak correction) to determine the statistical significance of the differences between populations in every body or head trait. Finally, discriminant analysis (DA, with Mahalanobis distances as the step inclusion method) was also applied to all traits (except SVL) in order to obtain information on which variables contributed more to differentiate the two sexes and populations.

Scaling and slope comparisons.—To elucidate the specific type of scaling relationships (isometric or allometric) between head and limb traits to SVL (or HL) of each sex from both populations, we applied regression analyses on $\log_{10}$ transformed data. Standard major axis regression (SMA, also called reduced major axis regression, RMA) was used to correct for random errors of dependent and independent variables (McArdle 1988; LaBarbera 1989). Deviations from isometry (slope = 1) were tested using SMA software (SMATR package, Falster *et al.* 2006). In a second step we performed intersex (within each population) and interpopulation (within each sex) comparisons of regression slopes. These comparisons were performed separately using head length and SVL as the covariate, and taking population or sex as factors. This method was used to independently consider the contribution of each of these traits to differences between males and females, and permitted us to compare our results with those previously found in other lizards (Kratochvil *et al.* 2003; Scharf & Meiri 2013). Slopes of each body trait to SVL (or HL) were compared by means of a test of heterogeneity in slopes included in the SMATR package. When this test detected a common slope, separate analyses (Wald test, SMATR package, Falster *et al.* 2006) were performed for male-to-female comparisons within each population and for within-sex interpopulation comparisons in order to detect shifts in elevation (residual axis scores) and shifts along an axis (fitted axis scores).

Significance level was always set at 0.05 and Sidak correction was used when applying multiple tests (Wright 1992).

RESULTS

Differences in Body Size

Table 1 shows (± S.E.), minimum, maximum values and sample sizes for the morphometric traits of males, females and juveniles of each population. SVL and TRL from one third of the largest individuals were not significantly different between populations (PERMANOVA, pseudo-F = 0.45, df = 1, p = 0.50 and pseudo-F = 1.36, df =1, p = 0.25, respectively) and they were significantly larger in males than in females (pseudo-F = 38.37, df = 1, p = 0.001, and pseudo-F = 32.83, df = 1, p = 0.001, respectively; Fig. 1(a) and (b)); the interaction (population × sex) did not have a significant effect on any trait (pseudo-F = 0.319, df = 1, p = 0.57, and pseudo-F = 0.15, df = 1, p = 0.70). Within-sex inter-population comparisons of those two traits did not show significant differences (p > 0.05 in all cases).

Morphological Differences between Populations and Sexes

MANCOVA showed there was a significant effect of the trunk length (covariate) on all morphological traits (Wilk's lambda = 0.066, $F_{5,91}$ = 259.05, p <0.001) and that there were significant differences in those traits between sites (Wilk's lambda = 0.45, $F_{5,91}$

Table 1. Mean, SE, minimum and maximum values, and sample sizes for the morphometric traits of the lizards from the two populations sampled.

	Sex		SVL	BM	TRL	HL	HW	HD	FLL	HLL
Tasartico	Males	Mean	146.84	94.59	110.30	36.54	17.66	19.57	50.31	77.96
		SE	6.81	12.43	4.95	1.91	1.03	1.35	1.96	2.84
		Minimum	88.00	22.00	66.10	21.90	10.85	9.45	33.00	52.50
		Maximum	220.00	224.00	161.50	58.50	30.10	32.50	63.94	110.00
		n	25	22	25	25	24	25	24	24
	Females	Mean	137.52	88.00	105.11	32.41	16.32	16.63	46.53	73.68
		SE	4.23	8.57	3.21	1.11	0.64	0.59	1.46	2.14
		Minimum	100.00	30.00	75.00	25.00	11.50	11.80	32.80	56.20
		Maximum	180.00	181.00	135.00	45.00	22.80	23.50	66.00	100.00
		n	23	21	23	23	23	23	22	23
	Juveniles	Mean	82.59	18.73	62.22	20.38	10.11	9.70	30.69	48.51
		SE	4.00	2.45	3.11	0.95	0.44	0.51	1.53	2.51
		Minimum	52.00	4.00	38.80	13.20	7.15	5.45	18.50	31.90
		Maximum	113.00	44.00	86.40	26.60	13.80	14.00	45.00	70.00
		n	22	22	22	22	21	22	22	21
Gáldar	Males	Mean	146.15	109.26	111.20	35.44	15.99	18.55	49.07	71.08
		SE	6.49	14.53	4.85	1.86	0.81	1.21	2.13	2.90
		Minimum	82.00	17.00	62.21	19.79	9.58	9.50	28.52	43.40
		Maximum	220.00	274.00	163.80	58.42	26.92	33.76	69.34	98.13
		n	34	31	33	33	33	33	33	33
	Females	Mean	140.35	83.82	108.27	32.07	14.70	16.16	46.65	65.48
		SE	3.60	6.51	2.76	0.89	0.43	0.51	1.05	1.45
		Minimum	105.00	34.00	80.94	23.60	11.06	11.14	36.60	52.91
		Maximum	170.00	145.00	129.98	40.02	18.38	21.56	58.06	86.55
		n	26	25	26	26	26	26	26	26
	Juveniles	Mean	90.15	20.71	69.25	20.90	9.83	10.59	31.53	48.12
		SE	3.84	2.39	2.99	0.87	0.41	0.52	1.46	2.03
		Minimum	69.00	8.00	52.95	16.05	7.28	7.01	23.50	36.57
		Maximum	108.00	36.20	83.77	24.60	11.75	12.86	38.46	58.21
		n	13	13	13	13	13	13	13	13

SVL, snout-to-vent length; BM, body mass; TRL, trunk length; HL, head length; HW, head width; HD, head depth; FLL, fore limb length; HLL, hind limb length.

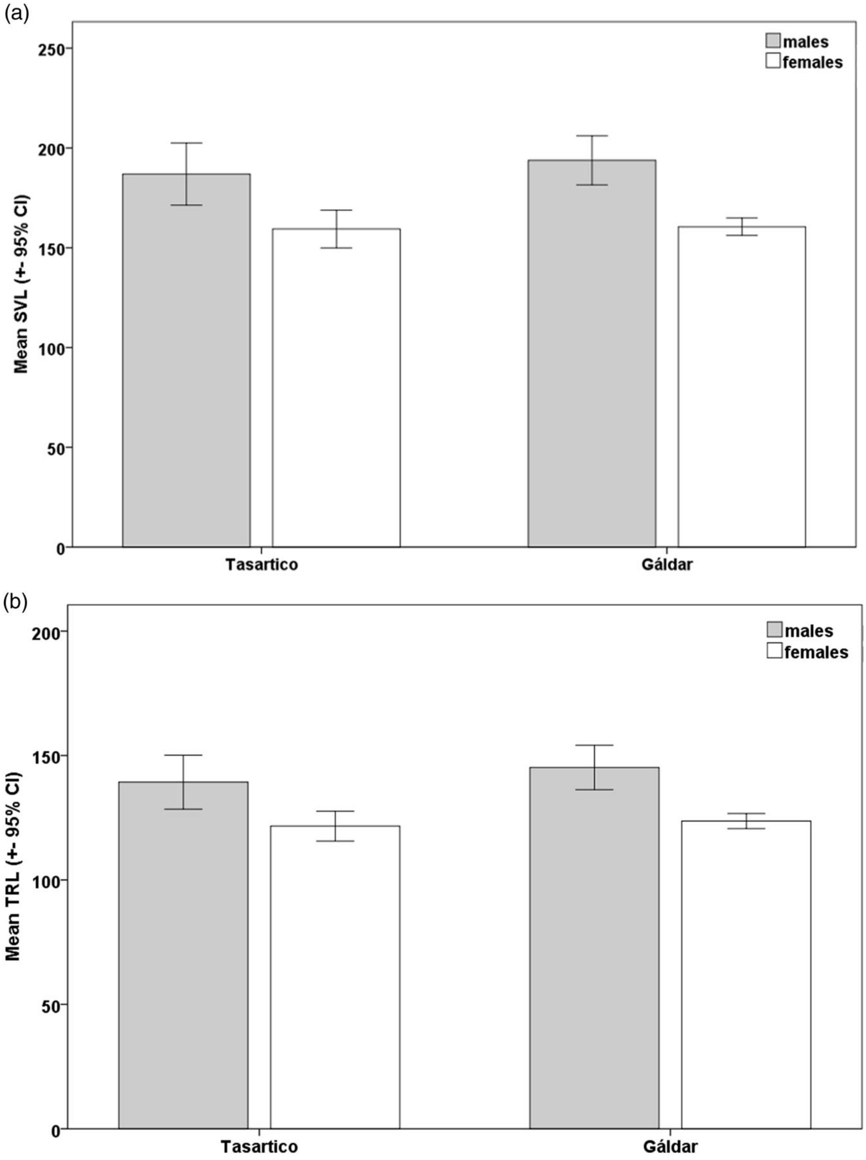

Figure 1. Mean values (± 95% CI) for (a) snout-to-vent length (SVL) and (b) trunk length (TRL) of males and females of both populations sampled.

= 26.41, p <0.001) and sexes (Wilk's lambda = 0.75, $F_{5,91} = 5.97$, $p < 0.001$) but no significant effect of their interaction (Wilk's lambda = 0.94, $F_{5,91} = 1.09$, $p = 0.37$). The posterior univariate analysis showed that these differences were mainly due to all traits (except FLL and HD) being significantly larger in Tasartico than in Gáldar population (Table 2), and all of them being significantly larger in males than in females (Table 2). No significant effect was found for the interaction of the two factors on any trait ($p > 0.05$ in all cases).

Table 2. Univariate comparison (univariate ANOVA) of morphometric traits between sites and sexes. (df: 1, 95; α = 0.025, after Sidak adjustment. Bold: significant values.

Source	Dependent variables	*F*	*p*
TRL (covariate)	**HD**	**516.10**	**<0.001**
	HW	**862.30**	**.<0.001**
	HL	**1279.45**	**<0.001**
	FLL	**628.10**	**<0.001**
	HLL	**391.76**	**<0.001**
Site	HD	3.97	0.049
	HW	**40.86**	**<0.001**
	HL	**7.69**	**0.007**
	FLL	2.56	0.113
	HLL	**51.95**	**<0.001**
Sex	**HD**	**16.79**	**<0.001**
	HW	**10.99**	**0.001**
	HL	**27.69**	**<0.001**
	FLL	**7.44**	**0.008**
	HLL	**7.35**	**0.008**
Site * sex	HD	0.59	0.442
	HW	0.002	0.968
	HL	0.14	0.700
	FLL	1.33	0.252
	HLL	0.60	0.438

TRL, trunk length; HD, head depth; HW, head width; HL, head length; FLL, fore limb length; HLL, head limb length.

Discriminant analysis showed two main significant functions (Wilk's lambda = 0.332 and 0.731, respectively) that explained 77.0 and 21.1% of data variance. HLL (having the highest correlation with the first function) was the trait that contributed most to differentiate between males and between females of the two populations, while the three head parameters (HD, HL and HW) between sexes within each population (Table 3 and Fig. 2).

Table 3. Traits that contributed most (in bold) to differentiate between the two lizard populations in each of the two significant canonical functions.

	Function	
	1	2
HLL	**0.284**	0.248
HD	0.060	**0.337**
HL	0.053	**0.301**
HW	0.171	**0.229**
FLL	0.036	0.226
TRL	-0.024	0.061

HLL, head limb length; HD, head depth; HL, head length; HW, head width; FLL, fore limb length; TRL, trunk length.

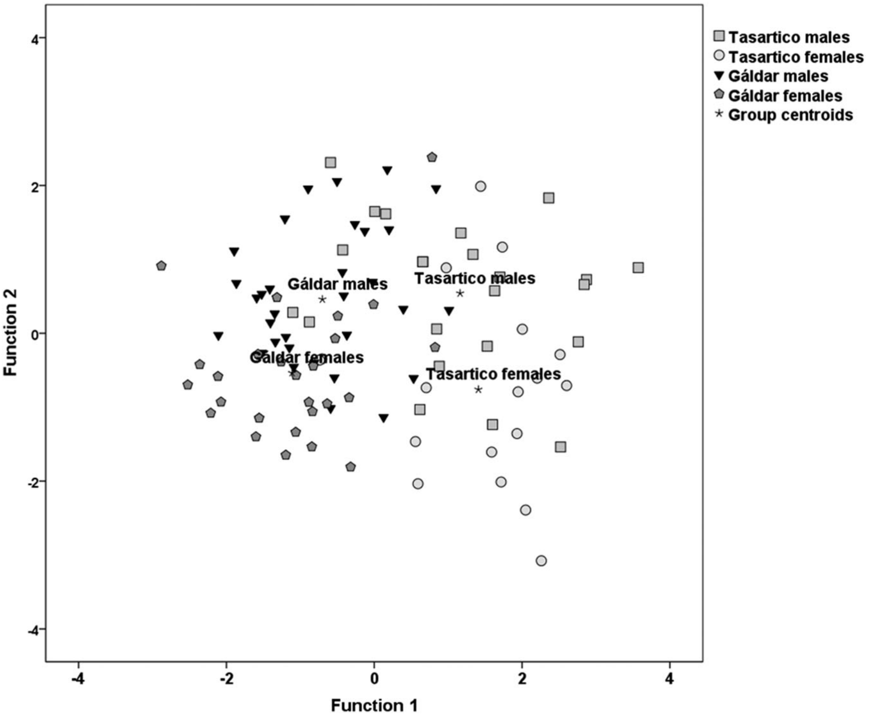

Figure 2. Scatter plot of the first and second discriminant functions obtained by the discriminant analysis applied to the morphological variables of males and females of the two populations.

Scaling Relationships

Significant regressions (positive or negative) were found relating SVL or HL to all other morphometric traits (Table 4 and Fig. 3(a), (b)). Significant positive allometries were detected for head parameters of males from both populations: HW and HD when regressed against SVL and HD when using HL as independent variable (Table 4). Significant negative allometries were found for HLL to SVL (and to HL) relationships in males from both sampling sites, and for FLL to HL relationship of males (Table 4).

The comparisons of slopes between sexes (Table 4, three right columns) showed that the major differences in both populations were: (a) females had relatively larger TRL than males both in relation to SVL and to HL; (b) males had a relatively larger HD than females in relation to SVL but not for its relationship to HL; (c) HLL was relatively larger in males than in females when related to SVL but not with HL. On the other hand, females from Tasartico had relatively larger HW and FLL in relation to HL than males, but not in those from Gáldar; and males from this last site had relatively larger HW than females in relation to SVL (Table 4).

The interpopulation comparison within each sex showed that HW and HLL were significantly larger (-shift in slope elevation- relatively to SVL and to HL) in males and females of Tasartico population than in those of Gáldar, while TRL was significantly larger (in relation to HL) in females of Gáldar than in those of Tasartico (Table 5). Other traits were not significantly different between populations except

Table 4. Statistics for regressions of morphological traits to snout-to-vent length (SVL) and to HL (SMA method) in males (m) and females (f) of each population (all significant, p <0.001). The comparison of each slope with 1 is included, indicating if it reflects positive or negative allometry and isometry; samples sizes: Tasartico: m = 23, f = 22; Gáldar: m = 32, f = 26. In bold: significant values after Sidak adjustment ($\alpha = 0.025$). The last three columns show the values of the Wald statistic for intersex slope comparison (shift in elevation of slopes), the p value and which sex has the relatively larger trait. In those cases where no difference in slope was found the values correspond to the t statistic from the heterogeneity of slopes test (*).

										Inter-sex slope comparison		
Site/trait	Covariate	sex	R^2	p	Slope	CI	F	p	Allometry	W	p	Larger sex
Tasartico												
TRL	**SVL**	**m**	**0.995**	**<0.001**	**0.969**	**0.941–0.998**	**4.668**	**0.041**	**Negative**	**4.13**	**0.042**	**F**
		f	0.98	<0.001	0.934	0.875–0.996	4.792	0.040	Negative			
	HL	m	0.942	<0.001	0.882	0.795–0.978	**6.326**	**0.019**	**Negative**	**8.97**	**0.003**	**F**
		f	0.788	<0.001	0.938	0.762–1.154	0.401	0.533	Isometry			
HW	SVL	m	0.961	<0.001	**1.167**	1.069–1.274	**13.535**	**0.001**	**Positive**	0.27*	0.598	None
		f	0.901	<0.001	1.171	1.003–1.367	4.615	0.046	Positive			
	HL	m	0.969	<0.001	1.054	0.976–1.138	1.987	0.173	Isometry	**5.93**	**0.015**	**F**
		f	0.933	<0.001	1.132	1.000–1.281	4.353	0.051	Positive			
HD		m	0.955	<0.001	1.474	1.345–1.616	80.312	**<0.001**	**Positive**	**6.75**	**0.009**	**M**
		f	0.423	<0.001	1.127	0.804	–1.581	0.525	0.477	Isometry		
		m	0.951	<0.001	1.341	1.219–1.476	**41.455**	**<0.001**	**Positive**	1.13*	0.26	None
		f	0.771	<0.001	1.185	0.955–1.470	2.656	0.118	Isometry			
FLL		m	0.814	<0.001	0.828	0.685–1.001	4.254	0.051	Isometry	1.91	0.14	None
		f	0.739	<0.001	0.936	0.739–1.185	0.337	0.568	Isometry			
		m	0.874	<0.001	0.752	0.643–0.879	**4.536**	**0.001**	**Negative**	**4.69**	**0.032**	**F**
		f	0.788	<0.001	1.003	0.811–1.241	0.001	0.972	Isometry			
HLL		m	0.830	<0.001	**0.772**	0.644–0.925	**8.841**	**0.007**	**Negative**	0.58*	0.434	None
		f	0.730	<0.001	0.910	0.715–1.157	0.654	0.428	Isometry			
		m	0.879	<0.001	0.701	0.601–0.818	**23.748**	**<0.001**	**Negative**	2.97*	0.079	None
		f	0.808	<0.001	0.873	0.712–1.069	1.927	0.180	Isometry			
Gáldar												
TRL		m	0.996	<0.001	0.964	0.942–0.986	**10.74**	**0.003**	**Negative**	Fs	**5.19**	**0.023**

	f	0.984	<0.001	0.997	0.945–1.053	0.09	0.927	Isometry			
	m	0.961	<0.001	0.849	0.789–0.912	**21.38**	**<0.001**	**Negative**	**14.94**	**<0.001**	**F**
	f	0.865	<0.001	0.918	0.787–1.071	1.29	0.266	Isometry			
HW	m	0.938	<0.001	1.099	1.003–1.203	**4.486**	**0.042**	**Positive**	**5.56**	**0.018**	**M**
	f	0.862	<0.001	1.168	0.999–1.365	4.219	0.051	Positive			
	m	0.965	<0.001	0.967	0.903–1.035	0.972	0.332	Isometry	1.50*	0.21	None
	f	0.858	<0.001	1.074	0.917–1.259	0.881	0.357	Isometry			
HD	m	0.922	<0.001	1.404	1.267–1.554	**47.25**	**<0.001**	**Positive**	**4.16**	**0.041**	**M**
	f	0.530	<0.001	1.193	0.897	–1.587	1.608	0.217	Isometry		
	m	0.934	<0.001	1.235	1.124–1.357	**21.21**	**<0.001**	**Positive**	0.81*	0.37	None
	f	0.657	<0.001	1.098	0.860–1.402	0.615	0.441	Isometry			
FLL	m	0.968	<0.001	0.968	0.905–1.036	0.938	0.340	Isometry	0.48*	0.47	None
	f	0.867	<0.001	0.918	0.785–1.074	1.250	0.275	Isometry			
	m	0.956	<0.001	0.852	0.789–0.920	**18.14**	**<0.001**	**Negative**	0.02*	0.88	None
	f	0.876	<0.001	0.842	0.726–0.976	5.78	0.024	Negative			
HLL	m	0.951	<0.001	0.896	0.825–0.973	**7.354**	**0.011**	**Negative**	**7.74**	**0.005**	**M**
	f	0.586	<0.001	0.850	0.646–1.118	1.473	0.237	Isometry			
	m	0.947	<0.001	0.788	0.725–0.857	**33.72**	**<0.001**	**Negative**	0.06*	0.81	None
	f	0.656	<0.001	0.764	0.598–0.975	5.18	0.032	Negative			

TRL, trunk length; HW, head width; HD, head depth; FLL, fore limb length; HLL, hind limb length.s

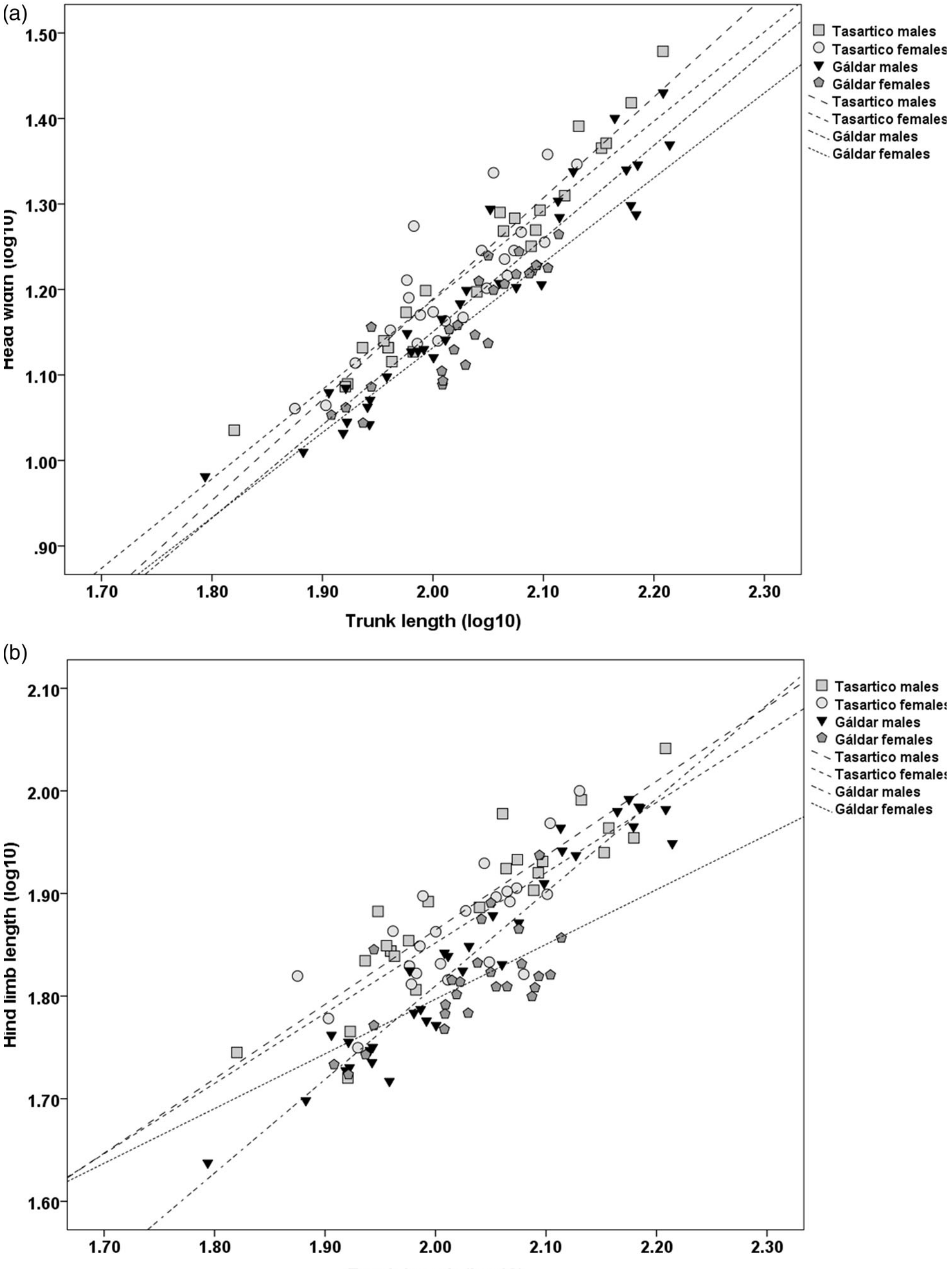

Figure 3. (a) Relationships of trunk length (TRL) to head width (HW) and (b) hind limb length (HLL) in males and females of Tasartico and Gáldar.

HD, which was significantly larger (relatively to SVL) in Tasartico males than in Gáldar males (Table 5).

Table 5. Within-sex interpopulation comparisons of slopes for the regressions of several morphological traits to SVL and HL. Values correspond to Wald statistic, p: signification level, and indication of which population had the relatively larger trait. All significant differences correspond to shifts in the elevation of slopes; non-significant values indicate no difference in slope (t statistic from heterogeneity of slopes test). T: Tasartico, G: Gáldar.

Covariate	TRL	HW	HD	FLL	HLL
Males SVL	**W = 6.34,** **$p = 0.012$** **(G > T)**	**W = 24.86 $p < 0.001$** **(T > G)**	**W = 4.24** **$p < 0.039$** **(T > G)**	W = 0.09 $p = 0.764$ (T = G)	**W = 26.16** **$p < 0.001$** **(T > G)**
HL	**W = 7.12,** **$p = 0.008$** **(G > T)**	**W = 16.41,** **$p < 0.001$** **(T > G)**	$t = 1.52$, $p = 0.22$ (T = G)	$t = 2.06$, $p = 0.14$ (T = G)	**W = 19.69,** **$p < 0.001$** **(T > G)**
Females SVL	$t = 2.48$ $p = 0.10$ (T = G)	**W = 35.18 $p < 0.001$** **(T > G)**	W = 0.035, $p = 0.851$ (T = G)	W = 0.007 $p = 0.933$ (T = G)	**W = 29.14** **$p < 0.001$** **(T > G)**
HL	**W = 4.25** **$p = 0.039$** **(G > T)**	**W = 22.81** **$p < 0.001$** **(T > G)**	$t = 0.22$ $p = 0.62$ (T = G)	$t = 1.86$, $p = 0.18$ (T = G)	**W = 40.7** **$p < 0.001$** **(T > G)**

SVL, snout-to-vent length; HL, head length; TRL, trunk length; HW, head width; HD, head depth; FLL, fore limb length; HLL, hind limb length.

Discussion

Between-sex and Population Comparison of Morphometric Traits

In both populations one third of the largest males attained significantly larger SVL and TRL than the same range of females. This sexual size dimorphism agrees with the result from intersex SVL comparison in another population of *G. stehlini* (Aldea Blanca, in the southeast of the island, Carretero *et al.* 2006) and with those from several other *Gallotia* species (Molina-Borja *et al.* 1997, 2010; Molina-Borja 2003, when mean or asymptotic SVL were considered). Male and female-biased SVL dimorphism but also monomorphism exists within Lacertidae (Cox *et al.* 2007; Ljubisavljević *et al.* 2008; Luo *et al.* 2012) and there is also evidence of within species variation (Roitberg 2007; Roitberg *et al.* 2015). Sexual selection, fecundity selection and natural selection have been traditionally considered the evolutionary factors affecting current SSD (see Anderson 1994 and Fairbairn 1997 for reviews; Olsson *et al.* 2002). For example, a higher intra-male sexual competition in certain habitats could have led to increased selection for bigger size in this sex (Carothers 1984; Stamps *et al.* 1997).

However, other major forces have been considered for explaining SSD in reptiles (see Censky, 1996; Cox *et al.* 2007, for review; Bonneaud *et al.* 2015): (1) proximal factors such as different male and female growth before and/or after maturation, (2) ecological factors such as varied demography and/or animal abundances. Different male and female post-maturation growth has not been yet documented in *G. stehlini*, but it has been reported for other Canarian lizards (Castanet & Báez 1991; Rodríguez-Domínguez *et al.* 1998); therefore, the larger maximum body lengths attained by adult males documented for this species could be accounted for in part by this proximal factor (Shine 1990; Stamps 1993).

On the other hand, a higher lizard density (and concomitant high intra-male competition) can contribute to a larger body size (Calsbeek & Smith 2007) and, in some cases, to a larger SSD as a significant positive association between both parameters was found in a phylogenetic study of several *Anolis* species (Stamps *et al.* 1997). No quantitative data exist on lizard densities for the two populations of *G. stehlini* studied, but their potential effect is not reflected in adult body size as no inter-population difference was detected in SVL of largest males or females.

On the other hand, multivariate comparison showed that, taking into account TRL, individuals from Tasartico had significantly larger HW, HL and HLL than those of Gáldar. Multivariate analysis of lizard morphological traits has previously shown differences among several populations associated to habitat traits (Butler & Losos, 2002), but the causes for the differences in *G. stehlini* cannot be ascertained at present using just two populations (Garland & Adolph 1994). Nevertheless, some ecological traits are different between habitats of each population. Both of them are near the coast, that of Gáldar in the northwest and that of Tasartico to the southwest of the island, which implies cooler and more humid weather (potentially having an influence on thermal availability) in the first compared to the second site. Moreover, vegetal food supply was more restricted—less shrubs per unit area—in the population of Tasartico than in Gáldar, the latter including *Opuntia* fleshy fruits (commonly consumed by lizards, Molina-Borja 1986). Therefore, these ecological differences could be factors that may have affected lizard growth and life-history patterns (Huey & Pianka 1981). The significantly larger HW and HLL in *G. stehlini* from Tasartico (southwest) suggests that evolutionary and ecological factors have acted more strongly on these traits in lizards from this site in comparison with those of Gáldar (northwest). Relatively larger HW could reflect higher intra-sexual competition in both sexes of Tasartico (see Table 5) than in Gáldar. Relatively larger HLL in the more open habitat (south) than in the closed one (north) agrees with what has been found in many lizard species (Losos *et al*. 2000; Melville & Swain 2000; Kohlsdorf *et al*. 2001; Schulte *et al*. 2004; Molina-Borja *et al*. 2010), and it has been interpreted as providing advantages in locomotion, foraging and escaping from predators in more open habitats (Bauwens *et al*. 1995; Melville & Swain 2000; Kohlsdorf *et al*. 2001; Herrel *et al*. 2002).

Moreover, in relation to TRL, males had significantly larger traits than females. This is a common result in many other lizard species including *Gallotia* (see below the discussion of sexual dimorphism in head size). Complementing the previous results, discriminant analysis permitted to conclude that the main traits contributing to differentiate between populations were HLL (first function) and several head parameters between sexes (second function).

Scaling Relationships for Body Traits

Results showed that head size (HW and HD) of males from both populations and HW for females of Tasartico had the only positive allometries when related to SVL (and/or HL, Table 4). On the other hand, the opposite relationships between trunk and head sizes in each sex (taking HL as covariate) were expected taking into account the larger contribution of trunk length to body size demonstrated in many female lizards (Braña 1996; Fairbairn 1997; Zamudio 1998; Scharf & Meiri 2013; Roitberg *et al*. 2015), and related to an evolutionary advantage (increased reproductive output) for the trait in this sex (Olsson *et al*. 2002).

Adult males with relatively larger heads occur in many lizard species (Carothers 1981; Cooper & Vitt 1989; Braña 1996; Thompson & Withers 2005; Kaliontzopoulou *et al.* 2007) and it has been interpreted as a result of sexual selection favouring this trait for intra-sexual fights and/or intersexual encounters (Carothers 1984; Hews 1990; Anderson & Vitt 1990, but see Shine 1991; Molina-Borja *et al*. 1998); males of *G. stehlini* fiercely bite each other's head during agonistic encounters (unpublished own data) and also males bite the female's neck during copulation (characteristic of all *Gallotia*, Böhme & Bischoff 1976). An alternative, but non-exclusive, hypothesis is that head size could also result from natural selection contributing to avoiding intersexual feeding competition (Schoener *et al*. 1982; Herrel *et al.* 1999; Shine *et al*. 2002); this hypothesis remains to be examined in *G. stehlini*, but several studies in *Gallotia* and other lacertid species show an evolutionary association of head morphology, bite force and diet in females, and suggests sexual selection as a more probable cause for head shape in males (Herrel *et al.* 1999; Kaliontzopoulou *et al*. 2012; López Darias *et al*. 2014). In *G. stehlini* a large head (with strong jaw muscles) may also function as a good antipredator weapon: when cornered by a human predator, individuals face him/her, open their mouths and emit at the same time a multi-frequency squeak (Böhme *et al.* 1985; Márquez & Cejudo 2000; own observations).

We also detected significantly larger TRL (in relation to HL) in both sexes from Gáldar than in those of Tasartico. For northern females this could indicate a relatively larger space available to developing eggs (Olsson *et al*. 2002) but it is not clear the meaning of the difference in TRL for males. However, the data indicate that individuals from both populations differ in two specific aspects of shape: relatively larger heads but smaller trunk lengths in Tasartico than in Gáldar.

On the other hand, the significant negative allometry of FLL and HLL to HL observed in each sex of Gáldar population indicates a proportionately smaller increase of limbs in relation to head size. However, this was evident only for Tasartico males. As the slopes of FLL or HLL to HL were not significantly different between sexes in any population (except for females from Tasartico, which had relatively larger fore-limb lengths than males), those two traits increase at a similar rate in both sexes. Previous comparative analysis of all *Gallotia* species showed that larger species had comparatively shorter hind limbs (in relation to SVL) than smaller species (Molina-Borja & Rodríguez-Domínguez 2004). Should this contribute to relatively lower sprint speed in the largest individuals (within a species) or the largest species? This seems not to be the case for among species comparison as at least absolute sprint speeds were higher in larger than smaller *Gallotia* species (Márquez & Cejudo 1997). Relatively larger hind limb lengths could contribute to attain a high sprint speed (Bauwens *et al*. 1995; Melville & Swain 2000; Kaliontzopoulou *et al.* 2013; Zamora-Camacho *et al.* 2014) that should have fitness consequences as a way of escaping from predators (Schulte *et al*. 2004; Husak & Rouse 2006) or be related to trophic ecology (Edwards *et al*. 2013). A direct relationship has been found between sprint speed and survival in hatchling lizards, with survivors having significantly larger hind limb lengths than non-survivors (Husak 2006).

Predators may affect the evolution of lizard morphology and behaviour (HLL and sprinting speed, Gifford *et al.* 2008). Potential predators at our sites during the sampling times could be kestrels, shrikes, common buzzards, cats, even long-eared owls, but there is no reference to their densities in different parts of the island. However, as habitat is more open at Tasartico than in Gáldar, predator pressure could be expected to be more intense in the first site.

It has been commonly found that male lizards have relatively larger hind limbs (in relation to SVL) than females (Lappin & Swinney 1999; Molina-Borja 2003; Molina-Borja *et al*. 2010). This has usually been interpreted as a trait contributing to higher running speeds and/or fighting abilities in males (Huey *et al*. 1984; Garland *et al.* 1990; Garland & Losos 1994; Bauwens *et al*. 1995; Lappin & Swinney 1999). However, when we considered HL instead of SVL as the covariate, the allometric difference in hind limb length between sexes disappeared (except for HLL to SVL relationship of individuals from Gáldar; see Table 4). This result is explained because considering SVL as the only measure of body size does not takes into account the relatively larger trunk and smaller heads of females, and is in line with similar results reported for other lacertids (Braña 1996; Kratochvíl *et al*. 2003; Scharf & Meiri 2013).

Acknowledgements

Miguel A. Carretero for providing useful suggestions for a first version of the text. We thank Consejería de Medio Ambiente of the Cabildo of Gran Canaria (island institution) for the permit to collect the animals.

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Received: 4 November 2015; Final acceptance: 8 December 2015