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ABSTRACT.—**We compared sexual dimorphism of body and head traits from adult lizards of populations of *Gallotia caesaris* living in ecologically different habitats of El Hierro and La Gomera. Males had larger body sizes than females, and sexual size and shape dimorphisms were greater in a population from La Gomera than in three populations from El Hierro. Multivariate analyses of variance, using linear and shape-adjusted traits, showed that the populations differed significantly in body and head traits, with pileus (head) width, snout–vent length (SVL), and body mass the main traits contributing to the differences. Males had larger SVL, heads, and limbs than females in all populations, but SVL relative to a shape index (calculated as the geometric mean of several body parameters) was larger in females than in males. Moreover, shape-adjusted hind-limb lengths were significantly shorter in lizards from the more densely vegetated habitats than in those from the less vegetated ones. The magnitude of sexual dimorphism was larger for relative limb length and head depth in the populations with less vegetation than in those with more vegetation. Our data suggest that morphological differences between populations reflect local adaptation to habitat structure.**

Geographic variation in morphological, physiological, or behavioral traits may reflect adaptation and evolutionary processes at the local scale. A variety of organisms have been analyzed in this context (see Emerson and Arnold, 1989), and within reptiles, populations of several lizard species have been studied (Losos, 1990; McCoy et al., 1997; Butler and Losos, 2002). Variations in patterns of sexual dimorphism in body size (SBSD), for example, are common and may include the following: (1) males having larger snout–vent length (SVL) than females (Carothers, 1984); (2) females having larger SVL lengths than males (Fitch, 1978; Zamudio, 1998); or (3) no sexual body dimorphism (Schwarzkopf, 2005). Other body and head traits may also exhibit sexual dimorphism (Cooper and Vitt, 1989).

Sexual dimorphism may result from different selective forces acting separately on each sex (Shine, 1989; Andersson and Vitt, 1990; Andersson, 1994; Fairbairn, 1997). Thus, a higher competitive ability, important for male reproductive success, is often associated with larger and stronger males (Stamps, 1983), but in species where female reproductive output increases with body size, females are often larger than males (Cooper and Vitt, 1989; Shine, 1989; Olsson et al., 2002). However, sexual dimorphism may also be caused by ecological, demographic, or ontogenetic causes (Schoener et al., 1982; Shine, 1990; Stamps et al., 1997; Le Galliard et al., 2006) and may express itself to different degrees in separate geographical locations (Madsen and Shine, 1993; Krause et al., 2003; Cox and John-Alder, 2007).

Analyses of sexual dimorphism have commonly used linear measurements of the body, head, or limbs (Cooper and Vitt, 1989; Hews, 1990; Fairbairn, 1997; Lappin and Swinney, 1999). However, analyses of shape dimorphism may provide very useful information and often reveal patterns that differ from those evident from analyses of sexual dimorphism in linear traits (Emerson, 1994; Braña, 1996; Butler and Losos, 2002).

Previous analyses have compared populations or species of *Gallotia* (Thorpe and Báez, 1987; Thorpe and Brown, 1991; Molina-Borja et al., 1997; Molina-Borja and Rodríguez-Domínguez, 2004). A phylogenetic analysis of variation in morphological traits in all *Gallotia* species showed that male to female SVL ratio (SBSD) did not change over evolutionary time in the Archipelago (Molina-Borja and Rodríguez-Domínguez, 2004). But geographical variation of morphological traits and body shape, as well as relationships between them and ecological characteristics, has not been analyzed for *Gallotia caesaris*. However, we predicted that the magnitude of SBSD could differ within each species because of differences in the degree of sexual selection, natural selection, or ecological

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Table 1. Percentage of soil covered by different plants and substrate types along transects in the sites of *Gallotia caesaris* sampling. Gcc: *Gallotia caesaris caesaris*; Gcg: *Gallotia caesaris gomerae*.

	Sargos (Gcc)	Guinea (Gcc)	Dehesa (Gcc)	Tecina (Gcg)
Kleinia	4.0	2.8	30	0
Euphorbia	0	3.7	27	0
Rumex	23.1	12.2	0	0
Schizogine	0	0	10	0
Rubia	0	0	15	0
Artemisia	4.7	27.8	2	0
Cistus monspeliensis	0	0	4	0
Messerschmidia	0	1.3	0	0
Gramineans (small grasses)	1	0	5	15
Stones	62.1	3.9	7	0
Sandy	4.1	0	0	0
Loamy	1.0	0	0	0
Lapilli	0	40.8	0	0
Stone wall	0	7.5	0	24.5
Fallen dry leaves (banana)	0	0	0	60.5

Table 2. Factor loadings of principal component analysis applied to the matrix of vegetation and substrate type coverage of the four habitats (see Table 1).

Sampling sites	PC1	PC2
Los Sargos	0.625	0.258
Guinea	0.390	0.732
Dehesa	0.434	−0.781
Tecina	−0.835	0.129
% explained variance	35.69	30.73

processes at a local scale. Therefore, the aim of the present work is to provide quantitative information on variation of SBSD and sexual dimorphism of head and body traits for populations of *G. caesaris* differing in the vegetative structure of their microhabitat. To that end, we examined sexual dimorphism in four populations of *G. caesaris*, one of *Gallotia caesaris gomerae* and three of *Gallotia caesaris caesaris*, living in areas with varied ecological characteristics. Hypothesizing stronger selective pressures in habitats with fewer resources that could have led to competitive advantage for larger males, we expected higher SBSD in the more severe habitats of *G. caesaris*. However, taking into account previous results for other lizard species and habitats (e.g., Herrel et al., 2001), and the differences in habitat structure between our study sites, we expected to find larger relative limb lengths in individuals of *G. caesaris* from the more open habitat (less vegetation) of Los Sargos in comparison with those from more closed (high vegetation density) ones of La Dehesa and Guinea.

Materials and Methods

Gallotia caesaris caesaris (from El Hierro Island) and *G. c. gomerae* (La Gomera) are small lizards (mean adult male SVL around 75 and 96 mm, respectively; Molina-Borja and Rodríguez-Domínguez, 2004) compared to other *Gallotia* species (for a detailed review of the Canarian lizard species, see Bischoff, 1998). According to genetic analyses (Thorpe et al., 1994), *G. c. caesaris* is closely related to *G. c. gomerae*, and both may be descendent from an ancestral *Gallotia galloti* like lizard.

We used pitfall traps baited with tomato and banana pieces to capture animals in the localities of Tecina (*G. c. gomerae*, southeast of La Gomera), and Guinea, Los Sargos and La Dehesa (*G. c. caesaris*, northwest and west of El Hierro, respectively), during breeding seasons (April to July) from 1999 to 2001. Lizard data were obtained at two different years only for the Guinea population. We pooled all data for this population because lizards were not resampled (marked by toe-clipping), and we did not find significant between-year differences in their traits.

We used variation in coverage by different plants and type of substratum as a measure of habitat diversity for each population. Because adult *Gallotia* lizards are preferentially herbivorous (Valido and Nogales, 1994), the degree of vegetative coverage also reflects food availability. We calculated coverage as the percentage of the ground covered by each plant species and by each substratum type (Table 1). To characterize habitat differences in vegetation covering and substrate type, we performed a principal component analysis (PCA) on the matrix of Table 1 (after arcsine-square-root transformation of the data).

We present the number of collected males and females in each population in Table 2. We considered individuals to be adults when their body size exceeded the minimum body size at sexual maturity for each sex of each subspecies. This minimum body size corresponds to the smallest male having well-developed hemipenes (62.0 and 77.1 mm SVL, respectively, for *G. c. caesaris* and *G. c. gomerae*) and the smallest female (57.0 and 73.6 mm, respectively) having developing eggs. One author argues that SBSD should be analyzed using asymptotic size (Stamps, 1993); however, estimates of this parameter in free-living animals are difficult (Stamps and Andrews, 1992). For our analyses here, we used only animals larger than the size at sexual maturity (Molina-Borja and Rodríguez-Domínguez, 2004). Estimates of SBSD based on asymptotic sizes (or 90th percentile, see Brown et al., 1999) did not differ appreciably from those obtained with our whole data samples.

The following biometric traits were measured for each individual: SVL, body mass (BM), pileus width (PW, head width measured at posterior end of parietal cephalic scales), head depth (HD), and fore- and hind-limb lengths (FLL, HLL, distances between groin and distal end of longer finger from each limb). We measured body mass with a small electronic balance (0.1 g precision) and biometric traits with a caliper (0.01 mm precision) in the field. After measurements, we released all animals unharmed at their capture site.

We used nonparametric tests when data were not normally distributed. Significance level was set at 0.05, but for multiple tests, a simultaneous Bonferroni correction was used (Chandler, 1995). Sexual size dimorphism was calculated using raw data with the formula of Lovich and Gibbons (1992) as (mean adult male body size / mean female body size) − 1. Data were analyzed using the SPSS 14.0 package.

Recent analyses provided evidence that some commonly used size-adjusting methods for among-population studies of morphological variation are not statistically adequate (McCoy et al., 2006). For example, analysis of covariance (ANCOVA) is based on the assumption of small variance in the covariate (body size), and residual analysis assumes that scaling relationships are equal among the groups (populations). Moreover, use of the first principal component (PC) of pooled data to be regressed against each trait also assumes similar scaling relationships among groups. Because there were large variances in body size, and the scaling relationships between head or body traits and SVL were different for the four populations of the present study (data not shown), we decided not to use residual values from pooled population data or PC-values for our analyses. However, we could not use the method advocated by McCoy et al. (2006) because the available program (R-environment: http://www.zoo.ufl.edu/bolker/R/windows/) only permits comparisons between two populations.

Therefore, we performed comparisons among populations, using linear and shape-adjusted body and head traits in separate analyses (see below). We used multivariate analysis of variance (MANOVA, with population and sex as fixed factors) and discriminant analysis (DA) to obtain a global view of population differences; DA also allowed us to determine which body or head traits contributed more to the differences among the four populations. We also used univariate statistical analyses (ANOVAs with post hoc Bonferroni testing) to determine one-to-one interpopulation statistical differences in every body or head trait. Because males and females of the four *G. caesaris* populations differed significantly in SVL, we used relative trait sizes (in relation to SVL, arcsine-square-root transformed) for the analyses of linear traits, after first testing that these data were not skewed or strongly nonnormal.

Shape-adjusted trait values were obtained using Mosimann's (1970) method (see also Butler and Losos, 2002) by calculating the geometric mean of an index of individual size (SIZE: fourth root of the product of SVL, CMASS [cubic root of mass], FLL, and HLL). Next, data from each individual were size adjusted by taking the difference of each $\log_{10}$-transformed variable with $\log_{10}$-transformed SIZE. Adjusting SVL in this way provides the contribution of body size to shape for each sex and population. We first verified that the distributions of these ratio data were not highly skewed or nonnormal. We incorporated this type of analysis because it can provide important information on intersexual and among-population variation in lizard body shape. The corresponding results may be different from those obtained through analyses of linear traits including SBSD. Sexual shape dimorphism was calculated using mean adult male SIZE / mean female SIZE) − 1 (Lovich and Gibbons, 1992).

RESULTS

Habitat Characteristics.—*Gallotia caesaris gomerae* that we studied live on a stone wall separating banana fields, with a greatly reduced number of wild plants. Along one side of the wall, fallen dry leaves of banana covered the ground, and along the other side was an unpaved road. The three populations of *G. c. caesaris* differed in substrate type and local vegetation. In Los Sargos, stones and ''calcosa'' (*Rumex lunaria*) plants covered a large percentage of the substratum. In Guinea, lapilli soil and ''incienso'' (*Artemisia canariensis*) were dominant (see Table 1). By contrast, a high diversity of vegetative cover occurred at the La Dehesa population, with ''verode'' (*Kleinia neriifolia*), ''tabaiba'' (*Euphorbia regis-jubae*), ''tasaigo'' (*Rubia fruticosa*), ''jara'' (*Cistus monspeliensis*), and ''sabina'' (*Juniperus turbinata*) as the primary species. Principal Component Analysis (PCA) of the habitat data from Table 1 shows differences between the four populations. Los Sargos and Tecina have very different plant and soil type coverings (opposite loadings along the first principal component, Table 2), and Guinea and Dehesa also differ as shown by opposite loadings along the second component.

Sexual Size and Shape Dimorphism.—Sample sizes, mean data (± standard error), and range for some linear and shape trait are displayed in Table 3. Body sizes were significantly larger in males than in females of the four populations (univariate ANOVA, population effect: $F_{3,274} = 98.62$; $P < 0.00001$; sex effect: $F_{1,274} = 59.62$; $P < 0.0001$; interaction effect: $F_{3,274} = 3.77$; $P = 0.011$; Fig. 1A). Body sizes were also larger in both sexes of *G. c. gomerae* than in those of the three populations of *G. c. caesaris* (Table 3 and Fig. 1A). However, shape-adjusted SVL was larger in females than in males of all populations (Fig. 1B). SBSD was 0.152 for *G. c. gomerae* and 0.082 for *G. c. caesaris* from Los Sargos population, 0.072 for that of Guinea and 0.069 for that of La Dehesa (Fig. 2). Sexual shape dimorphism (SShD) showed the same pattern, being largest in the first subspecies (0.194) and lower in the three populations of the second (0.123, 0.098 and 0.039, respectively, Fig. 2). Therefore, *G. c. gomerae* (Tecina population) with the larger body size had SBSD and SShD greater than those of the other three populations (*G. c. caesaris*) with smaller body sizes. A positive relationship between SBSD or SShD and SVL did not hold within the three populations of *G. c. caesaris*, because the population with larger body size has a smaller SBSD or SShD than those with smaller body sizes; however, there is a significant inverse relationship between SBSD (or SShD) and vegetation covering in the three populations of *G. c. caesaris* ($r = 0.99$, $P < 0.01$; Fig. 2).

Comparisons of Relative and Shape-Adjusted Trait Sizes.—Multivariate analysis of variance (MANOVA) using all morphological linear traits showed significant differences among populations ($F_{18,663} = 41.513$; $P < 0.001$), between sexes ($F_{6,219} = 52.416$; $P < 0.001$), and for the interaction of population and sex ($F_{18,663} = 4.011$; $P < 0.001$). The same type of analysis for shape-adjusted traits also showed significant differences among populations ($F_{21,711} = 37.061$; $P < 0.001$), sexes ($F_{7,235} = 43.746$; $P < 0.001$), and the interaction of population and sex ($F_{21,711} = 2.988$; $P < 0.001$).

When male and female traits were analyzed separately, one-way ANOVA showed significant among-population differences in body size and linear and shape-adjusted traits within each sex ($P < 0.001$ in all cases; see Table 4 for every within sex and among population trait comparison).

Sexual Dimorphism in Head and Limb Traits.—Clear sexual dimorphism was evident in head and limb traits. Thus, relative size and shape-adjusted PW and HD were significantly larger in males than in females, except in the population of *G. c. caesaris* from Los Sargos (Fig. 3A, B, Table 5).

Relative sizes of FLL and HLL were significantly larger in males than in females of Los Sargos and Guinea populations but not in the other two (Fig. 4A). However, when considering shape-adjusted values for FLL and HLL, a significant dimorphism was present only for HLL in *G. c. caesaris* from Los Sargos population (Fig. 4B, Table 5). Across populations, relative size and shape-adjusted HLL were significantly larger in both sexes of Los Sargos population (*G. c. caesaris*) than in the other three populations ($P < 0.001$ in all cases, Fig. 4B).

Discriminant Analysis.—As canonical structure was very similar when analyzed separately for males and females of the four populations, we obtained the structure for all adult individuals based on all traits (Table 6, Fig. 5). The extracted canonical variables explained 88.6% and 69% of variance (function 1, for shape-adjusted and linear measurement analyses, respectively) and 10.8% and 26.5% (function 2). Individuals from the Los Sargos population separated from those of the other three populations (Fig. 5). The traits that contributed most to differentiation among populations were shape-adjusted HD, PW, and BM (function 1) and BM, SIZE, FLL, and HLL (function 2, Table 6).

Relationship of Limb Lengths with Vegetative Coverage.—Relative and shape-adjusted HLL were significantly larger in males and females from Los Sargos and Guinea (with less vegetation covering) than in those from La Dehesa and Tecina (with high vegetation covering) (males: $t_{129} = 6.95$, $P < 0.0001$, and $t_{134} = 4.99$, $P < 0.0001$, respectively; females: $t_{137} = 3.61$, $P = 0.0004$, and $t_{96} = 3.01$, $P = 0.003$, respectively).

DISCUSSION

Sexual Dimorphism in Body Size and Shape.—Males and females of *G. c. gomerae* (Tecina population) had larger body lengths than those of the three populations of *G. c. caesaris* from El Hierro, and both SBSD and SShD were greater in the first subspecies than in the three populations of the second one. Within some taxa, a positive scaling relationship exists between adult body size and the magnitude of SBSD (Rench's rule, see Fairbairn, 1997). Our results fit this rule, *G. c. gomerae* having a larger body size and a larger SBSD and SShD than *G. c. caesaris*. This relationship does not hold for the three populations of *G. c. caesaris*, because the population (La Dehesa) with larger SVL did not have the higher SBSD, and it agrees with a phylogenetic analysis of all species of *Gallotia* (Molina-Borja and Rodríguez-Domínguez, 2004).

TABLE 3. Sample size (*N*), means, SE, and range of linear measurements of some body and head traits and of shape-adjusted traits (Sa) for males (m) and females (f) of the four populations of *Gallotia caesaris*. BM: body mass, HD: head depth, FLL: forelimb length.

		BM (g)		Sa-BM		HD (mm)		Sa-HD		FLL (mm)		Sa-FLL	
Species (population)		m	f	m	f	m	f	m	f	m	f	m	f
G. c. caesaris (Guinea, El Hierro)	*N*	49	49	49	49	49	49	49	49	49	49	49	49
	Mean	11.77	8.33	−0.95	−0.95	9.15	7.7	−0.34	−0.37	25.68	22.94	0.10	0.10
	SE	0.55	0.36	0.002	0.003	0.15	0.09	0.003	0.003	0.30	0.22	0.002	0.003
	Range	6, 21	4, 14	−0.99, 0.90	−1.0, −0.91	7.5, 12.1	6.1, 9.1	−0.40, −0.28	−0.41, −0.33	20.6, 31.7	19.4, 26.8	0.08, 0.15	0.06, 0.16
G. c. caesaris (Los Sargos, El Hierro)	*N*	30	33	30	33	30	33	30	33	30	34	30	33
	Mean	14.03	9.88	−0.97	−0.96	10.94	8.94	−0.31	−0.35	30.28	26.61	0.13	0.13
	SE	0.67	0.33	0.003	0.002	0.18	0.13	0.004	0.004	0.34	0.32	0.004	0.003
	Range	6, 21	7, 16	−1.00, −0.92	−1.0, −0.93	9.1, 12.5	7.2, 10.1	−0.37, −0.27	−0.40, −0.29	27.0, 34.1	21.8, 29.5	0.09, 0.17	0.09, 0.17
G. c. caesaris (La Dehesa, El Hierro)	*N*	38	26	32	26	38	26	38	26	38	27	38	27
	Mean	14.50	11.35	−0.93	−0.94	9.24	8.04	−0.34	−0.37	25.99	24.17	0.10	0.10
	SE	0.81	0.65	0.002	0.003	0.22	0.17	0.002	0.002	0.59	0.37	0.002	0.002
	Range	5, 26	6, 19	−0.93, −0.90	−097, −0.90	6.62, 12.06	6.14, 9.85	−0.41, −0.27	−0.46, −0.28	18.6, 36.4	19.3, 27.5	0.04, 0.17	0.05, 0.17
G. c. gomerae (Tecina, La Gomera)	*N*	22	28	22	28	23	29	22	28	23	29	22	27
	Mean	28.59	16.29	−0.93	−0.94	11.3	8.7	−0.36	−0.39	32.29	26.6	0.09	0.09
	SE	1.85	0.73	0.003	0.004	0.31	0.09	0.005	0.004	0.70	0.35	0.002	0.002
	Range	12, 39	10.0, 25.0	−0.97, −0.91	−0.97, −0.88	8.4, 13.0	7.7, 9.5	−0.40, −0.32	−0.46, −0.35	25.8, 36.9	21.2, 26.9	0.08, 0.12	0.07, 0.11

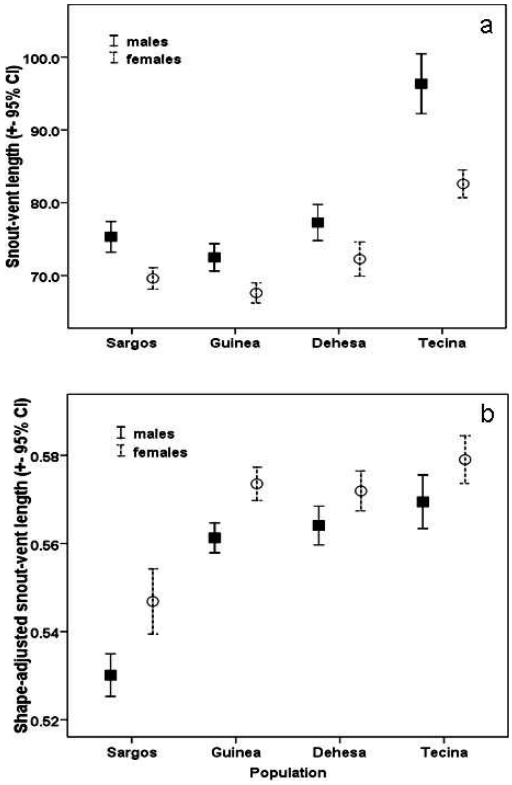

FIG. 1. Mean (± 95% CI) SVL (a) and body shape (b) of males (black squares) and females (open circles) of the four populations studied.

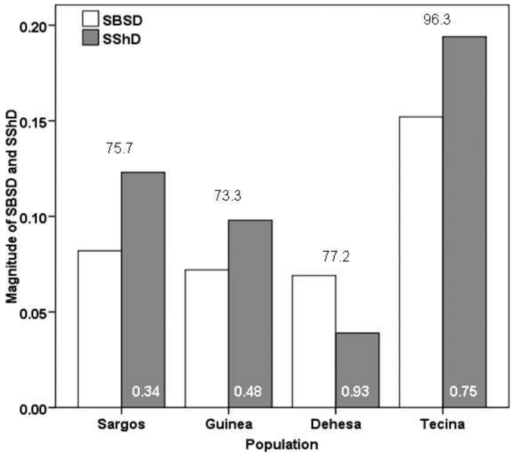

FIG. 2. Sexual body size (SBSD) and shape (SShD) dimorphism in the four lizard populations studied. Numbers above each pair of bars correspond to mean male SVL. Numbers inside bars correspond to vegetation covering (%) of each sampling site.

Different evolutionary factors may contribute to SBSD, including the intensity of male–male competition, the effect of mate choice, and the effect of natural selection for body or specific sex traits (see review of Andersson, 1994). Because there is no effect of allometry on SBSD in the populations of *G. caesaris*, an important factor for the differences in SBSD could be a higher intensity of intramale competition in habitats with low resources (Stamps et al., 1997). Butler et al. (2000) suggested competition with respect to structural habitat and sexual selection pressures as the most likely causes of SBSD variation in *Anolis* ecomorphs of the Greater Antilles, but a phylogenetic analysis of 309 lizard species from 18 different families (including the Lacertidae) found a weak overall relationship between SBSD and male aggression or other measures of sexual selection (Cox et al., 2003).

Another evolutionary factor that may influence SBSD is the presence of other sympatric lizard species (Poe et al., 2007). The much larger *Gallotia simonyi* and *Gallotia bravoana* lived at the same time as *G. caesaris* on El Hierro and La Gomera, respectively. Thus, competition with the larger species could have affected the evolution of body size and shape and, therefore, the magnitude of SBSD in *G. caesaris* on each island.

Local (ecological) factors may also have been acting, as the magnitude of SBSD and SShD exhibit an inverse relationship with the vegetative coverage of the three populations of *G. c. caesaris* (Fig. 2). This suggests that the mechanisms underlying the expression of sexual dimorphism act differently among habitats. Genetic and ecological traits such as differential growth (Cox and John-Alder, 2007), mortality rates, and food resource use between males and females are known to affect body size differences between populations (Houston and Shine, 1993; Wikelski and Trillmich, 1997). We found different male and female growth trajectories in the larger species *G. simonyi* (Rodríguez-Domínguez et al., 1998). If *G. caesaris* follows the same pattern, a proximal mechanism for SBSD could be sexually dimorphic growth.

Sexual Dimorphism in Relative Size or Shape-Adjusted Head and Body Traits.—Adult males from the four populations are larger and more robust than females, but female SVL relative to shape is larger than that of males (Fig. 1B). This also occurs in several *Anolis* species (Butler and Losos, 2002) and emphasizes the importance of considering body shape in addition to body size (Schwarzkopf, 2005). A relatively larger trunk length in females confers additional space for egg development (Braña, 1996), and a positive

TABLE 4. Significance level of one-to-one interpopulation comparisons (with Bonferroni correction) of linear (A) and shape-adjusted (B) traits from males (m) and females (f). See trait abbreviations in text. *P*: significance level; n.s.: nonsignificant difference.

	Gcc (“Guinea”)		Gcg (“Tecina”)		Gcc (“La Dehesa”)	
	P		*P*		*P*	
	m	f	m	f	m	f
(A)						
Gcc (“Sargos”)						
SVL	n.s.	n.s.	<0.001	<0.001	n.s.	n.s.
PW	<0.001	0.020	<0.001	n.s.	n.s.	n.s.
HD	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
FLL	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
HLL	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
CI	0.002	n.s.	n.s.	n.s.	n.s.	n.s.
Gcc (“Guinea”)						
SVL			<0.001	<0.001	n.s.	<0.001
PW			n.s.	<0.001	0.001	<0.001
HD			<0.001	<0.001	n.s.	n.s.
FLL			0.057	0.047	n.s.	n.s.
HLL			n.s.	n.s.	n.s.	n.s.
CI			n.s.	n.s.	0.004	0.014
Gcg (“Tecina”)						
SVL					<0.001	<0.001
PW					<0.001	n.s.
HD					n.s.	0.028
FLL					n.s.	n.s.
HLL					n.s.	n.s.
CI					n.s.	n.s.
(B)						
Gcc (“Sargos”)						
SVL	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
PW	<0.001	<0.001	<0.001	<0.001	<0.001	n.s.
HD	<0.001	0.002	<0.001	<0.001	<0.001	<0.001
FLL	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
HLL	<0.001	0.049	<0.001	0.002	<0.001	0.004
BW	<0.001	n.s.	<0.001	<0.001	<0.001	<0.001
Gcc (“Guinea”)						
SVL			0.074	<0.001	n.s.	n.s.
PW			n. s.	0.002	<0.001	<0.001
HD			0.062	<0.001	n.s.	n.s.
FLL			0.082	0.009	n.s.	n.s.
HLL			n.s.	n.s.	n.s.	n.s.
BW			0.004	0.007	<0.001	0.014
Gcg (“Tecina”)						
SVL					n.s.	n.s.
PW					<0.001	n.s.
HD					n.s.	0.051
FLL					n.s.	n.s.
HLL					n.s.	n.s.
BW					n.s.	n.s.

relationship exists between female SVL and clutch size in several lizard species including *Gallotia* (Molina-Borja and Rodríguez-Domínguez, 2004). Moreover, the relative size of SVL in relation to shape is smaller in both sexes of *G. c. caesaris* from Los Sargos than that of all the other populations (Fig. 1B). Los Sargos has volcanic lava substrate and sparse vegetation, representing lower resource availability for lizards. This ecological constraint may determine a lower capacity to reach larger body sizes (Wikelski et al., 1997).

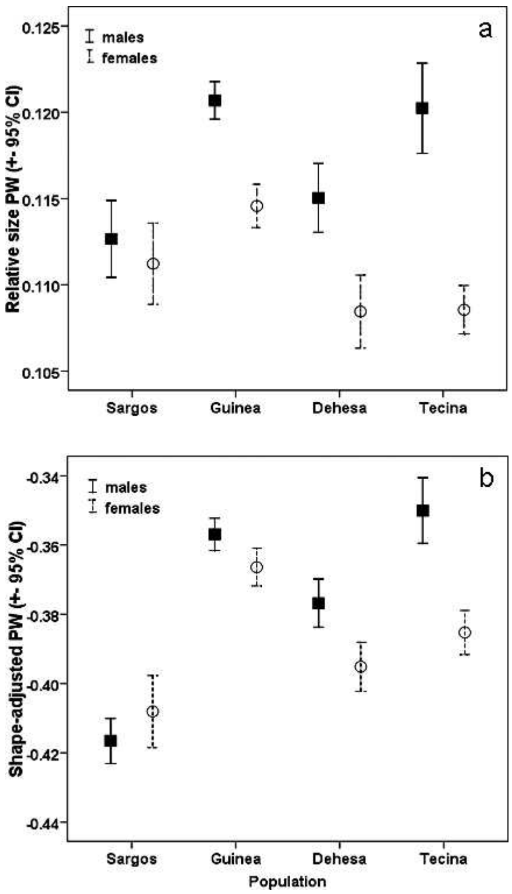

FIG. 3. Mean (± 95% CI) PW (a) and shape-adjusted PW (b) of males (black squares) and females (open circles) of the four populations studied.

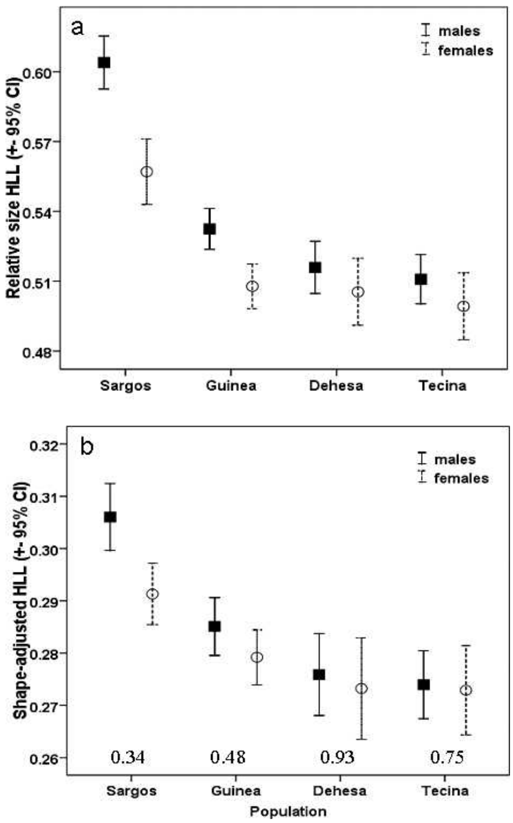

FIG. 4. Mean (± 95% CI) HLL (a) and shape-adjusted HLL (b) of males (black squares) and females (open circles) of the four populations studied. Numbers under bars correspond to vegetation covering (%) of each sampling site.

Sexual dimorphism was also found for relative- and shape-adjusted head size in all populations, PW and HD being significantly larger in males than in females, except PW for the Los Sargos population (Fig. 3A, B). Larger head size in males than in females is common in several lizard species (Carothers, 1984; Vitt and Cooper, 1985; Hews, 1990) and likely contributes to a higher probability of winning fighting contests (Hews, 1990; Molina-Borja et al., 1998), possibly because of a higher biting force associated with larger heads (Herrel et al., 1999; Lailvaux et al., 2004; Huyghe et al.,

TABLE 5. Results of male to female comparisons (one-way ANOVA) of linear and shape-adjusted (Sa-) traits in the four populations studied.

	G. c. caesaris (Los Sargos, El Hierro)		*G. c. caesaris* (Guinea, El Hierro)		*G. c. caesaris* (La Dehesa, El Hierro)		*G. c. gomerae* (Tecina, La Gomera)	
	F	*P*	*F*	*P*	*F*	*P*	*F*	*P*
PW	1.36	0.25	60.85	<0.001	23.84	<0.001	78.1	<0.001
Sa-PW	1.35	0.25	7.67	0.007	14.03	<0.001	46.33	<0.001
HD	47.0	<0.0001	100.41	<0.001	27.82	<0.001	60.28	<0.001
Sa-HD	36.8	<0.0001	28.37	<0.001	18.61	<0.001	36.79	<0.001
FLL	5.84	0.019	13.27	<0.001	0.87	0.35	4.76	0.03
Sa-FLL	0.71	0.40	0.84	0.36	0.0001	0.99	1.52	0.22
HLL	25.42	<0.0001	16.38	<0.001	2.3	0.13	1.57	0.21
Sa-HLL	12.04	0.001	3.18	0.078	0.24	0.62	0.09	0.75

TABLE 6. Standardized coefficients of the canonical discriminant functions obtained from the analysis of shape-adjusted measurements of all specimens from the four populations studied.

	Function		
Trait	1	2	3
SIZE	0.335	−1.029	−1.011
PW	0.630	−0.272	0.641
HD	−0.911	0.365	0.253
FLL	−0.292	0.827	0.012
HLL	0.075	0.689	0.004
BM	0.574	1.945	0.559

2005). Intramale aggression is high in *G. caesaris* during breeding periods; thus, sexual selection on head size has likely contributed to the observed dimorphism. A phylogenetic analysis of eublepharid lizards showed an association of head dimorphism with the presence of male combat (Kratochvíl and Frynta, 2002). Niche divergence hypothesis was ruled out for head dimorphism in the close *G. galloti* (Herrel et al., 1999), but this possibility cannot be discarded without a specific analysis for *G. caesaris*.

Hind-limb size (HLL) was significantly larger in males than females, with the exception of shape-adjusted HLL in La Dehesa and Tecina populations (Fig. 4A, B). This agrees with observations for other lizard species (Lappin and Swinney, 1999), including *Gallotia* (Rodríguez-Domínguez et al., 1998; Molina Borja, 2003). Relatively larger HLL in males is typically related to greater movement capacity and speed (Losos, 1990; Christian and Garland, 1996; Gifford et al., 2008), mating ability, or increased ability to fight (Lappin and Swinney, 1999). Results extrapolated from four *Gallotia* species (Márquez et al., 1997) show that species having relatively longer HLL also have higher maximum sprint velocities. Males of *G. caesaris* patrol their home ranges during breeding and could benefit from higher sprint speeds achieved through their longer limbs.

Interpopulation Differences in Relative Size and Shape-Adjusted Traits.—Both relative and shape-adjusted sizes of HD, FLL, and HLL were relatively larger in males in the Los Sargos population than in the other three (Table 3 and Fig. 4). Because head depth is related to bite force (Herrel et al., 1999; Huyghe et al., 2005), this result could indicate greater intrasexual selection acting on lizards from Los Sargos, which is characterized by an environment with fewer resources relative to the other populations (Table 1).

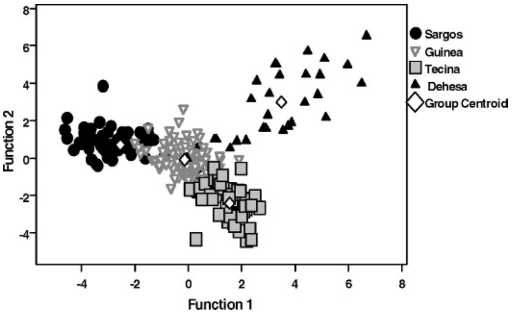

FIG. 5. Scatter plot of the first and second canonical variables obtained by the discriminant analysis applied to the morphological—shape-adjusted variables—data of all populations.

Other causes of the differences in relative trait sizes or shapes between the populations of *G. caesaris* may be caused by local adaptation or phenotypic plasticity. Thus, shape-adjusted HLL was significantly larger in males and females from Los Sargos and Guinea with less vegetation covering than in the densely vegetated La Dehesa and Tecina. Therefore, we suggest this may result from different ecological pressures affecting the evolution of lizards in open or closed habitats. This is supported by data showing persistent differences in climbing speed of juveniles obtained from females of three ecologically distinct populations of the closely related *G. galloti* (Vanhooydonck et al., 2001; but see Vanhooydonck and Van Damme, 1999). Comparative analyses in several lizard taxa also found larger limbs and higher sprinting ability in species inhabiting open habitats than in those of closed ones (Garland and Losos, 1994; Bauwens et al., 1995; Losos et al., 2000; Melville and Swain, 2000; Herrel et al., 2001; Kohlsdorf et al., 2001; Schulte et al., 2004; Calsbeek and Irschick, 2007).

Discriminant analysis revealed that the Los Sargos population is clearly separated from the others (Fig. 5, Table 5). Because the Los Sargos site is characterized by a more open habitat structure, the difference in morphology could be the result of different selective pressures related to habitat use.

Overall, our results agree with other reports of relationships between geographical variation in type of habitat and morphological variation in different species and populations (Malhotra and Thorpe, 1997; Knox et al., 2001). Although several factors (from genetic ones to phenotypic plasticity; Losos et al., 2000) may be involved in the expression of morphological variation in different geographical localities, analyses on *Anolis* species suggest a crucial role of natural selection rather than phenotypic plasticity (Thorpe et al., 2004, 2005). In our case, even populations of *G. c. caesaris* from sites not very distantly separated but with different ecological characteristics show significant differences in morphology. Here, we demonstrate a significant difference in the relative and shape-adjusted size of hind limbs between populations that live in habitats with different vegetative covering. Our data suggest that this pattern could reflect local adaptation to habitat structure.

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