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Morphological variation in *Gallotia atlantica* from the volcanic island of Lanzarote: subspecies designations and recent lava flows

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A detailed uni- and multivariate analysis of within-island geographical variation in scalation and body dimensions of the lacertid lizard, *Gallotia atlantica*, from Lanzarote (and two neighbouring offshore islets) was carried out. Two main morphological groupings were detected: four populations clustered within a putative *malpaís* group, i.e. from relatively recent volcanic lava fields (seven populations were sampled from these areas), while the other 19 populations (including the three remaining *malpaís* populations, and those from the offshore islets of Montaña Clara and Alegranza) also clustered together. Thus, while there is a tendency for occupation of *malpaís* areas to be related to morphological variation, this model does have some inconsistencies. The differentiated *malpaís* group comprises populations from two geographically isolated areas, one from the central-western part of the island (Timanfaya) and the other from the north (Malpaís de la Corona). The divergence of these populations is considered to have arisen recently, rather than their being relicts of an ancient, formerly widespread, lineage. The morphological variation partially supports the previous use of two different subspecies to describe the within-island variation. However, if such a scheme were applied then one of the subspecies would need to encompass populations from the geographically separated southern Timanfaya and Malpaís de la Corona areas, as opposed to just the latter. We reject previous observations that either *malpaís* individuals in general, or those corresponding to the north-eastern subspecies, are larger than individuals from other areas. The pattern of morphological variation of *G. atlantica* within Lanzarote is less pronounced but shows some similarities with patterns of morphological variation in lizards from neighbouring islands.

ADDITIONAL KEYWORDS: Canary Islands – evolution – lizard – morphology – population – volcano.

INTRODUCTION

The Canary Islands, an oceanic group of seven main islands and several smaller islets, have become a model region for studies of both between- and within-island patterns of geographical variation, particularly in lizards (e.g. Brown, Campos-Delgado & Pestano, 2000; Gübitz, Thorpe & Malhotra, 2000; Juan *et al.*, 2000, and references therein; Pestano & Brown, 1999; Richard & Thorpe, 2001; Thorpe & Richard, 2001). The islands lie between 110 and 500 km off the coast of north-west Africa and were independently formed by volcanic eruptions from the ocean floor over the past 20 Myr.

Lanzarote is found in the north-east of the archipelago and is one of the oldest islands. It has a surface area of 846 km^2 and rises to a maximum altitude of 670 m towards the north at Peñas de Chache. It is generally arid, with an annual rainfall of less than 200 mm in most areas, although slightly higher rainfall is found around the aforementioned peak. The most striking ecological heterogeneity within the island is not due to variation in rainfall and altitude, as on the nearby islands of Tenerife and Gran Canaria (Thorpe & Brown, 1989; Brown, Thorpe & Báez, 1991), but rather the different habitat types produced by expanses of solidified lava from relatively recent eruptions (Fig. 1).

Recent lava flows have given rise to *malpaís* (badlands) habitats. These are found in the central-west

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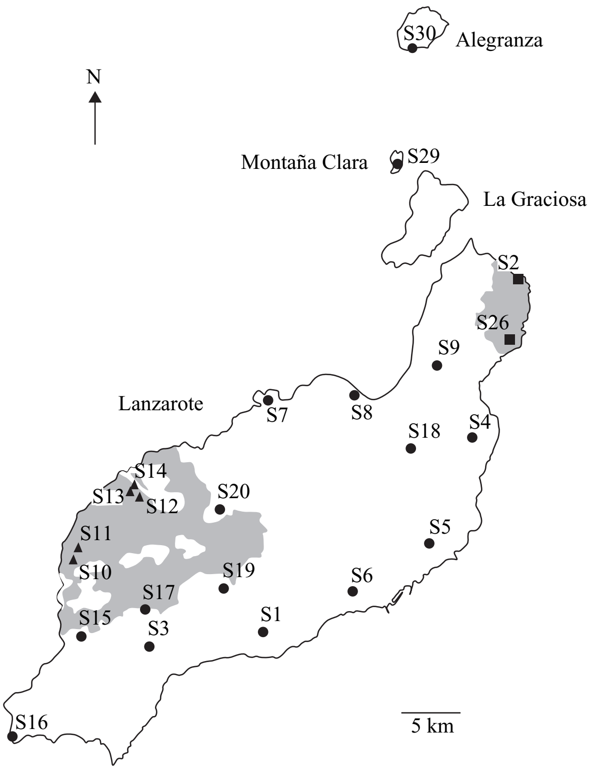

Figure 1. Distribution of sampling sites of *Gallotia atlantica* in Lanzarote and nearby islets. Site names and sample details are given in the Appendix. Shaded areas represent the main regions covered by relatively recent lava flows in central-western (Timanfaya) and north-eastern Lanzarote. Sites are indicated using circles, except for Malpaís de la Corona (squares) and Timanfaya (triangles). Sites within the latter, although ostensibly close in some cases (e.g. S12–14), were all from different exclusive 'islets' within the lava fields.

(Timanfaya) and north-east of the island (Malpaís de la Corona). The former was formed by lava flows from volcanic activity in the eighteenth and nineteenth centuries and contains several isolated areas (known locally as 'islets') that were not covered during these eruptions (Carracedo, Badiola & Soler, 1992). Malpaís de la Corona is considerably older (although still recent in geological terms), with lavas being dated at about 21 ka (Carracedo *et al.*, 2003) and is consequently in a more advanced state of ecological succession.

The unique biophysical conditions prevailing on the recent lava fields suggest that they represent novel and harsh environments to colonizing populations. The lacertid lizard *G. atlantica* (Peters & Doria, 1882), is quite abundant throughout most of the island, but is rare/absent on the Timanfaya lava fields (although present on the 'islets' within Timanfaya). Generally lower densities are found on Malpaís de la Corona.

Gallotia atlantica is known to exhibit considerable morphological variation in size, body proportions and scalation, as well as coloration and colour pattern (Bischoff, 1985a, b; Castroviejo, Mateo & Collado, 1985; Thorpe, 1985), the extent of which has resulted in the description of numerous subspecies. *G. a. atlantica* has been assigned to populations from the main island of Lanzarote and its northern offshore islets (Bischoff, 1985a; Castroviejo *et al.*, 1985), *G. a. laurae* to populations from north-eastern Lanzarote (Castroviejo *et al.*, 1985), and *G. a. ibagnezi* to the northern-most islet of Alegranza (Castroviejo *et al.*, 1985). Of these, the widespread northern (*G. a. atlantica*) and north-eastern Lanzarote (*G. a. laurae*) subspecies are generally accepted as conventional subspecies categories, while *G. a. ibagnezi* tends to be regarded as *G. a. atlantica* (López-Jurado, Mateo & Geniez, 1995).

Castroviejo *et al.* (1985) believed that the *G. a. laurae* subspecies designation was justified for populations from the lavas of Malpaís de la Corona and those found to the south-east of Haría based on morphological differentiation. However, Bischoff (1985a) preferred a single widespread northern (*G. a. atlantica*) subspecies. More recently, López-Jurado & Mateo (1992) appear to relate the distribution of *G. a. laurae* to areas of *malpaís*, and there is some evidence to support the similarity of individuals (primarily size, coloration and markings) from El Mojón and El Golfo in the Timanfaya area with the *G. a. laurae* (Malpaís de la Corona) subspecies (López-Jurado & Mateo, 1992; López-Jurado *et al.*, 1995).

These studies also indicate that individuals associated with recent volcanic habitats attain adult body sizes considerably greater than those from other parts of Lanzarote (Castroviejo *et al.*, 1985; López-Jurado & Mateo, 1992). Unfortunately, most of these proposals have been made on the basis of qualitative comparisons, and/or only partial sampling of the island. Thus the actual pattern of geographical variation, its potential causes, and the validity and utility of proposed taxonomic designations are still difficult to assess.

This paper provides a quantitative analysis of morphological variation in *G. atlantica* from Lanzarote based on a sampling regime that encompasses the full extent of morphological variation throughout the island and associated islets.

MATERIAL AND METHODS

SITES AND SPECIMENS

Adult lizards ($N = 460$) were captured and subsequently measured between August and September 1999, and in October 2002. Only adult animals (ten males and ten females from each site) were retained for measurement due to the difficulties of sexing younger individuals in the field. An individual was considered adult if it had a body size (snout–vent length) approaching or greater than the minimum size at sexual maturity documented for the northern (*G. a. atlantica*) subspecies: 59.5 mm for males and 57.0 mm for females (Molina-Borja, 2003). Sex was established by hemipenal inversion, with palpation of the abdomen used to identify gravid females.

The 21 capture sites within the main island of Lanzarote and those on the nearby offshore islets of Montaña Clara and Alegranza were selected to cover all major areas, habitats, and putative subspecies (Fig. 1, Appendix). Site S30 on the northern-most islet of Alegranza corresponded to the locality of ssp. *G. a. ibagnezi*. Sites S2 and S26 from the lavas of Malpaís de la Corona corresponded to *G. a. laurae*. More specifically, site S26 corresponded to one of the locations from which specimens were named as *G. a. laurae* by Castroviejo *et al*. (1985).

During fieldwork in the Timanfaya region, no individuals were observed or caught on areas of lava more than 1 m away from the 'islets'. Each site in this area corresponds to an individual isolated 'islet' within the *malpais*. Site S10 from Timanfaya corresponded to the area referred to as El Mojón, from which individuals of *G. atlantica* were reported by López-Jurado & Mateo (1992) to exhibit close morphological similarity to ssp. *G. a. laurae* of north-eastern Lanzarote. Lizards were trapped under licence using tomato-baited pitfall traps or by hand, and released at their point of capture within 24 h.

CHARACTERS

Morphology was recorded on captured live individuals. Seven scalation characters and two linear body measurements were recorded. The characters were chosen to include a subset of those used by Castroviejo *et al*. (1985) and for the reliability and ease with which they could be recorded in the field.

The seven scalation characters were: number of gular scales (GS), number of rows of ventral scales from the collar to the last complete row of ventral scales before the vent (VS), number of lamellae scales on the fourth rear hind toe (IDL), number of femoral pores on the underside of the rear hind limb (FP), number of upper-row lateral blotches along the side (ULB), number of scales across the widest point of the first lateral blotch (FBW), number of scales across the widest point of the second lateral blotch (SBW).

The two linear body measurements were: length from the tip of the snout to the anterior edge of the vent (snout–vent length, SVL), and head length from the tip of the snout to the posterior edge of the collar (HL). SVL was measured to the nearest 0.5 mm using a ruler and HL measured to the nearest 0.1 mm using Vernier callipers.

All bilateral characters were recorded from the right-hand side of the individual to avoid the influence of fluctuating asymmetry, and characters were recorded sequentially for each individual to minimize measuring error. FBW and SBW were approximated if the upper-lateral blotches had merged (males only). Each character was recorded twice, with a third measurement being taken if the first two differed.

STATISTICAL ANALYSES

The use of mean body size in among-population comparisons of size differences has been shown to be inappropriate because of its dependence on the underlying age structure of the population, which can exhibit considerable spatial and temporal variation in species with asymptotic growth after maturity (Stamps & Andrews, 1992; Stamps, 1993). The effects of age structure on geographical comparisons of body size can be alleviated using estimates of asymptotic body size (ABS) – the size at which somatic growth has stopped or become negligible (Stamps & Andrews, 1992; Brown *et al*., 1999). Estimates of typical ABS are usually obtained from capture-recapture data on individual growth rates (e.g. El Mouden, Znari & Brown, 1999), an impractical approach when a large number of sites are to be studied.

Alternative methods by which this can be achieved include the use of the largest individual per sample (Stamps & Andrews, 1992) and percentiles (Brown *et al*., 1999). Brown *et al*. (1999) have shown that the latter method can provide more accurate and precise estimates of ABS than the former, which tends to have an upward bias. In this study, the use of percentiles may bias ABS due to the fact that the larger individuals have been selected from each site. Thus the mean of the largest three individuals was used as an intermediate approach.

The prediction that populations of *G. atlantica* associated with recent volcanic habitat attain a larger size than those from other parts of Lanzarote (López-Jurado & Mateo, 1992) was assessed using nested analyses of variance (ANOVA) on SVL (site nested within ecotype). Populations with a close association with recent volcanic habitat were classified as *malpaís* sites, which included those from Malpaís de la Corona (S2 and S26), as well as the northern (S12, S13 and S14) and southern (S10 and S11) 'islet' sites from Timanfaya National Park and the surrounding area. Sites from all other parts of Lanzarote were classified as non-*malpaís*.

Geographic variation and sexual dimorphism in HL was assessed using a two-way ANCOVA (covariate SVL), and adjusted measurements of HL obtained for each individual based on the pooled within-group regression slopes. Two-way ANOVAs were applied to scalation characters. Normal plots and Levene's test of homogeneity of variances were used to explore the validity of the assumptions for these tests. Here and elsewhere, sequential Bonferroni corrections were used to adjust *P*-values to control Type I error rates in multiple comparisons across each set of analyses (Rice, 1989).

Correlation (product-moment) coefficients computed between each pair of characters and between sexes for a given character were used to test congruence of geographical patterns and pattern repeatability, respectively. Tests of homogeneity among the 23 within-site correlation coefficients (r) were computed using a test statistic that approximates to the chi-square distribution under the null hypothesis of no heterogeneity, and is based on Hotelling's transformation of r (see Brown, 1997). Heterogeneity among the 23 within-site character correlations was interpreted in terms of differences in character linkage.

Canonical variates analysis (CVA) was used to describe and summarize among-site differences in multivariate morphology (hereafter referred to as generalized morphology). CVAs on the 23 male and female sites were computed with all characters entered simultaneously. A CVA on the 23 male sites was computed using the characters HL, GS, VS, FP, IDL, ULB and FBW. Due to colinearity, SBW was not included in the analysis, while FBW was retained because it contributed most to among-site variation (ANOVA: highest F-value). A CVA on the 23 female sites was computed using the characters HL, GS, VS, FP, IDL, ULB, FBW and SBW.

Complementary principal component analyses (PCAs) were computed and the results compared to assess the robustness of CVAs. The PCAs were based on the correlation matrix (rather than the variance-covariance matrix) to achieve standardization of the variables. Site means of the same characters (untransformed) as those used in the male and female CVAs were used as the input for the PCA to achieve appropriate data reduction (James & McCulloch, 1990). Comparisons of PCA matrices (based on Euclidean distances computed between site PCA scores) with CVA matrices (based on Mahalanobis D^2 distances from the CVAs) were performed using the program Mantel (Liedloff, 1999) using 4999 random matrix associations. This produced maximum achievable significance values of 0.0002.

For ease of visualization, overall similarity among sites was portrayed using phenograms based on Mahalanobis D^2 distances. It should be noted that these are not intended to portray phylogenetic relationships but merely depict general phenetic grouping patterns based on the overall among-site morphological distances. The UPGMA method was used because of its tendency to maximize the correlation between structure of the input distance matrix and output dissimilarities and the resultant dendrogram (see McGarigal, Cushman & Stafford, 2000).

RESULTS

PATTERNS OF GEOGRAPHICAL VARIATION

Significant among-site variation was found for HL and all seven scalation characters, and between sexes for HL, VS, IDL, FBW and SBW (Table 1). Among-site variation in the degree of sexual dimorphism (interaction) was found for HL, IDL, FBW and SBW, but only HL, FBW, and SBW were significant after adjustment for multiple comparisons. Significant differences (nested ANOVA) were found in body size (SVL) between *malpaís* and non-*malpaís* populations in males ($F_{[1,189]} = 55.24$, $P < 0.001$) and females ($F_{[1,189]} = 6.59$, $P < 0.011$) within the main island.

Table 1. Summary results of two-way ANCOVA and ANOVAs. The F-ratios are given with the corresponding degrees of freedom for comparisons of geographical (site) and sexual dimorphism (sex), as well as geographical variation in sexual dimorphism (interaction). The significance level adjusted (table-wide) for multiple comparisons using the sequential Bonferroni technique is given. *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$

Character	Site	Sex	Interaction
HL	$F_{22,413} = 4.55$***	$F_{1,413} = 426.33$***	$F_{22,413} = 4.09$***
GS	$F_{22,414} = 8.08$***	$F_{1,414} = 0.54$	$F_{22,414} = 0.78$
VS	$F_{22,414} = 4.00$***	$F_{1,414} = 175.63$***	$F_{22,414} = 1.31$
FP	$F_{22,414} = 2.56$**	$F_{1,414} = 0.61$	$F_{22,414} = 0.84$
IDL	$F_{22,414} = 4.82$***	$F_{1,414} = 14.12$**	$F_{22,414} = 1.57$
ULB	$F_{22,414} = 6.01$***	$F_{1,414} = 0.32$	$F_{22,414} = 1.01$
FBW	$F_{22,414} = 2.38$**	$F_{1,414} = 183.93$***	$F_{22,414} = 2.35$**
SBW	$F_{22,414} = 2.30$**	$F_{1,414} = 156.25$***	$F_{22,414} = 2.21$*

Estimates of the pooled within-site correlations between pairs of scalation characters were generally low (i.e. $r < 0.5$) for males and females, except for FBW/SBW ($r = 0.80$, males) (Table 2). All character correlations were homogeneous across the sites; thus there is little evidence of among-site differences in character linkage among the scalation characters (Brown, 1997).

Congruence in among-site patterns of variation between individual characters for each sex was variable (i.e. $r < 0.5$) (Table 3), with the exception of ABS/FBW (males), ABS/SBW (males), GS/FP (males), GS/IDL (males and females), GS/ULB (males), GS/FBW (males), FP/IDL (males), FP/ULB (females), IDL/ULB (males), ULB/SBW (females), FBW/SBW (females), for which moderate (i.e. $r > 0.5$) correlation coefficients (product moment) were obtained; as well as GS/FP (females) and FBW/SBW (males) for which higher correlations (i.e. $r > 0.7$) were obtained. This suggests that geographical patterns of variation vary considerably between characters. Congruence between sexes was higher, providing support for the reliability of the patterns.

Variation in individual characters among the 21 male and female sites within the main island of Lanzarote was visualized on maps to identify any geographical patterns, i.e. mosaic, categorical or clinal. Almost all characters tended to show quite a mosaic pattern within the island, although site estimates of ABS showed quite a clear trend (Fig. 2B) (see later).

In terms of the significant difference (nested ANOVA) found in adult body size between *malpaís*/non-*malpaís* populations the general tendency is clearly the opposite to that claimed by previous studies with more restricted sampling regimes: *G. atlantica* from recent volcanic habitats actually attain smaller sizes than those from other parts of the island. In general, the largest sizes are found in the northern and southern regions, while the smallest adult body sizes are found in the central region, characterized by fine sandy soil and sparse vegetation and referred to locally as El Jable. Males and females from Montaña Clara attained a considerably smaller typical ABS than those from the main island, as did those from the northern-most islet of Alegranza (Fig. 2A). Although the absolute extent of the pattern of variation in typical ABS differs between males and females, the relative pattern was remarkably congruent ($r = 0.89$, $P < 0.001$).

Congruence (distance-matrix correlations) between CVA and PCA patterns of among-site divergence was high for both males ($r = 0.93$, $P < 0.001$) and females ($r = 0.91$, $P < 0.001$), indicating that the CVAs had not been significantly perturbed by possible heteroscedasticity or multivariate non-normality. Summary results of the relative contribution of the first three canonical vectors (CV1, CV2 and CV3) to within-site and among-site variation are shown in Table 4. The amount of among-site variation summarized by the first three canonical vectors was similar for males (75.8%) and females (72.2%).

In males, characters contributing most to CVs1–3 were as follows: CV1 (42.9%): GS, IDL, ULB and FBW; CV2 (19.0%): HL and VS; CV3 (13.9%): IDL, HL and VS. In females, they were as follows: CV1 (36.4%): HL, GS, FP and ULB; CV2 (21.0%): HL, GS and IDL; CV3 (14.8%): HL, GS and VS.

Visual inspection of the plots revealed that CV1 and CV2 do not show clear clines. However, values for CV1 (Fig. 3) were clearly divergent for the Malpaís de la Corona and southern Timanfaya populations for both males and females. Site S15, close to the southern Timanfaya populations, also clustered with this group for male CV1, but this pattern was not repeated for

Table 2. Pooled within-site correlation (product-moment) coefficients between pairs of scalation characters for males (M) and females (F)

		GS	VS	FP	IDL	ULB	FBW	SBW
GS	M		0.12	0.09	0.09	0.06	0.08	0.08
	F		0.14	0.17	0.16	0.05	–0.07	0.10
VS	M			0.14	0.21	–0.06	–0.08	–0.18
	F			–0.01	0.13	0.10	–0.16	0.05
FP	M				0.18	–0.05	0.04	0.02
	F				0.22	0.04	0.21	0.11
IDL	M					0.08	0.08	0.05
	F					0.04	0.10	0.14
ULB	M						0.04	0.13
	F						0.18	0.23
FBW	M							0.80
	F							0.47

Table 3. Congruence in the patterns of among-site variation: between individual characters for males (M) and females (F), and between sexes for each character (M + F). The significance level adjusted (table-wide) for multiple comparisons using the sequential Bonferroni technique is given. *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$

		ABS	HL	GS	VS	FP	IDL	ULB	FBW	SBW
ABS	M		–0.48	0.04	–0.20	–0.45	0.15	0.17	0.65	*0.66
	F		–0.23	0.22	–0.02	–0.06	0.43	0.06	0.04	0.10
	M + F	***0.89								
HL	M			–0.16	–0.09	–0.12	–0.25	–0.17	–0.18	–0.29
	F			0.18	–0.02	0.43	0.05	0.25	0.37	0.27
	M + F		0.51							
GS	M				0.41	0.52	0.63	*0.67	0.54	0.41
	F				0.25	**0.75	*0.66	0.44	0.25	0.33
	M + F			***0.83						
VS	M					0.43	0.10	0.31	0.12	0.20
	F					0.46	0.19	0.43	0.11	0.48
	M + F				0.51					
FP	M						0.53	0.28	–0.08	–0.15
	F						0.31	0.64	0.23	0.41
	M + F					0.51				
IDL	M							0.53	0.35	0.20
	F							0.42	0.38	0.46
	M + F						0.54			
ULB	M								0.46	0.33
	F								0.34	0.59
	M + F							**0.73		
FBW	M									***0.91
	F									0.64
	M + F								0.05	
SBW	M									
	F									
	M + F									0.01

Table 4. Summary results for CVA. Canonical vectors (CV) 1, 2 and 3 are shown for male (M) and female (F) sites. Canonical loadings, eigenvalues, percent variance, cumulative percent variance and squared canonical correlation (canonical correlation) are given

	CV1		CV2		CV3	
	M	F	M	F	M	F
HL	–0.214	0.475	0.556	–0.684	0.498	0.449
GS	0.694	0.451	0.299	0.489	–0.064	0.446
VS	0.164	0.320	0.497	0.097	–0.414	–0.619
FP	0.210	0.413	0.175	0.091	0.177	0.017
IDL	0.567	0.244	–0.188	0.398	0.556	0.283
ULB	0.438	0.588	0.231	0.253	–0.036	–0.300
FBW	0.364	0.202	–0.116	–0.088	–0.347	0.167
SBW	–	0.368	–	0.056	–	–0.134
Eigenvalue	1.006	0.779	0.444	0.449	0.326	0.316
% of variance	42.94	36.43	18.96	20.99	13.91	14.79
Cumulative %	42.94	36.43	61.90	57.41	75.81	72.21
Canonical correlation	0.50	0.44	0.31	0.31	0.25	0.24

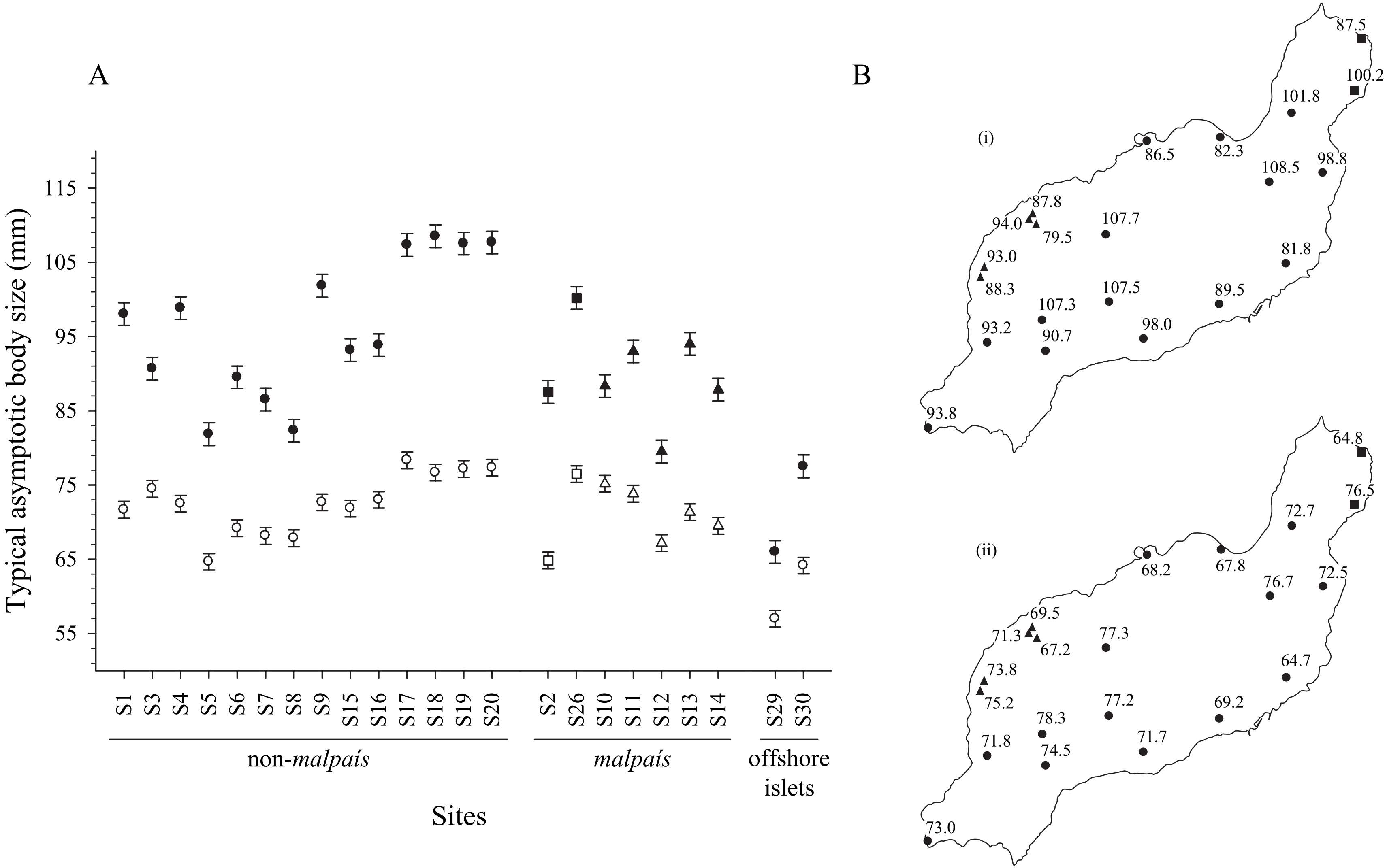

Figure 2. A, estimates of ABS for males (solid symbols) and females (empty symbols). Respective pooled within-site standard errors are 1.52 and 1.12. Symbols correspond to Fig. 1. B, geographical patterns of estimated ABS of adult male (i) and female (ii) *G. atlantica* from the main island of Lanzarote.

females. The morphological separation between sites is depicted in Figure 4. The presence of two discrete groupings is found in both males and females. Sites S2, S10, S26, and to a lesser degree S11, could be separated from the remaining 19 sites by the first two canonical vectors (61.9% and 57.4% of the total among-site variation for males and females, respectively). S2, S10, S11 and S26 could be subdivided further into two discrete groupings corresponding to S2 and S26, and to S10 and S11 by CV3 (13.9% and 14.8% of the total among-site variation for males and females, respectively). Groupings among the remaining 19 sites were inconsistent between the sexes; for example, S4 grouped with S6 in females, but it was quite distinct in males.

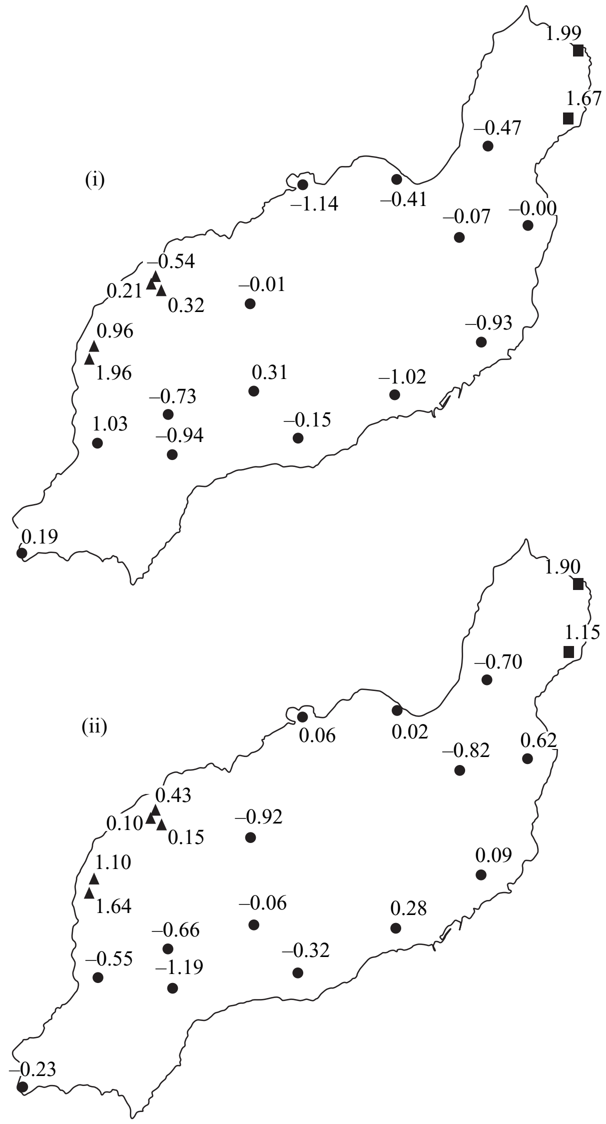

Figure 3. Patterns of geographical variation in site CVA scores: (i) male CV1, (ii) female CV1.

The UPGMA phenograms for the 23 male and female sites are shown in Figure 5. They reveal two distinct groupings concordant between males and females, supporting the delineation of two morphologically distinct groups. One morphotype is found throughout the main island of Lanzarote and on the islets of Montaña Clara and Alegranza, while the other is found in Malpaís de la Corona and southern Timanfaya.

DISCUSSION

As well as the substantial size variation, male and female *G. atlantica* exhibit considerable geographical variation in generalized morphology. While the absolute scale of resemblance differs between the sexes, the main patterns for males and females are remarkably congruent. The relationship between the geographical variation and the distribution of recent volcanic habitat within Lanzarote is broadly in agreement with that previously suggested, i.e. populations from areas associated with the recent lavas of Malpaís de la Corona and southern Timanfaya exhibit a degree of morphological similarity (López-Jurado & Mateo, 1992). However, we demonstrate that this is only true for two of the five Timanfaya populations studied. Why the northern Timanfaya populations do not belong to this phenetic grouping is difficult to ascertain if we

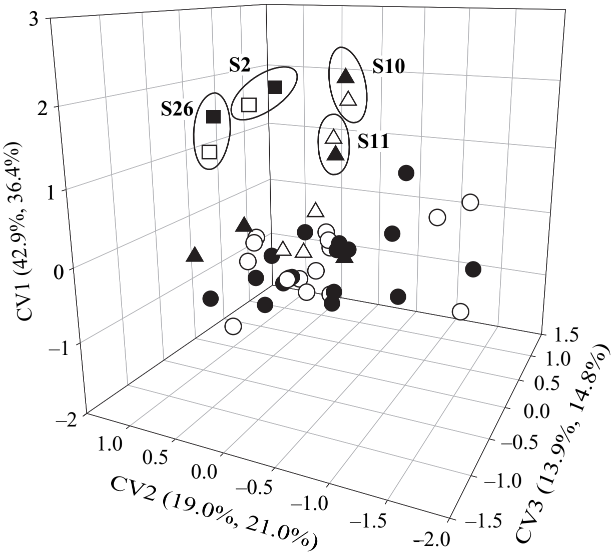

Figure 4. Canonical variate (CV) plots for the 23 male (solid symbols) and female (empty symbols) sites (based on single sex analyses). Site mean scores were evaluated on the first three unstandardized canonical vectors. The proportion of among-site variation for each axis (% male, % female) is shown. Respective contributions of CV1, CV2 and CV3 were 75.8% and 72.2% for males and females, respectively.

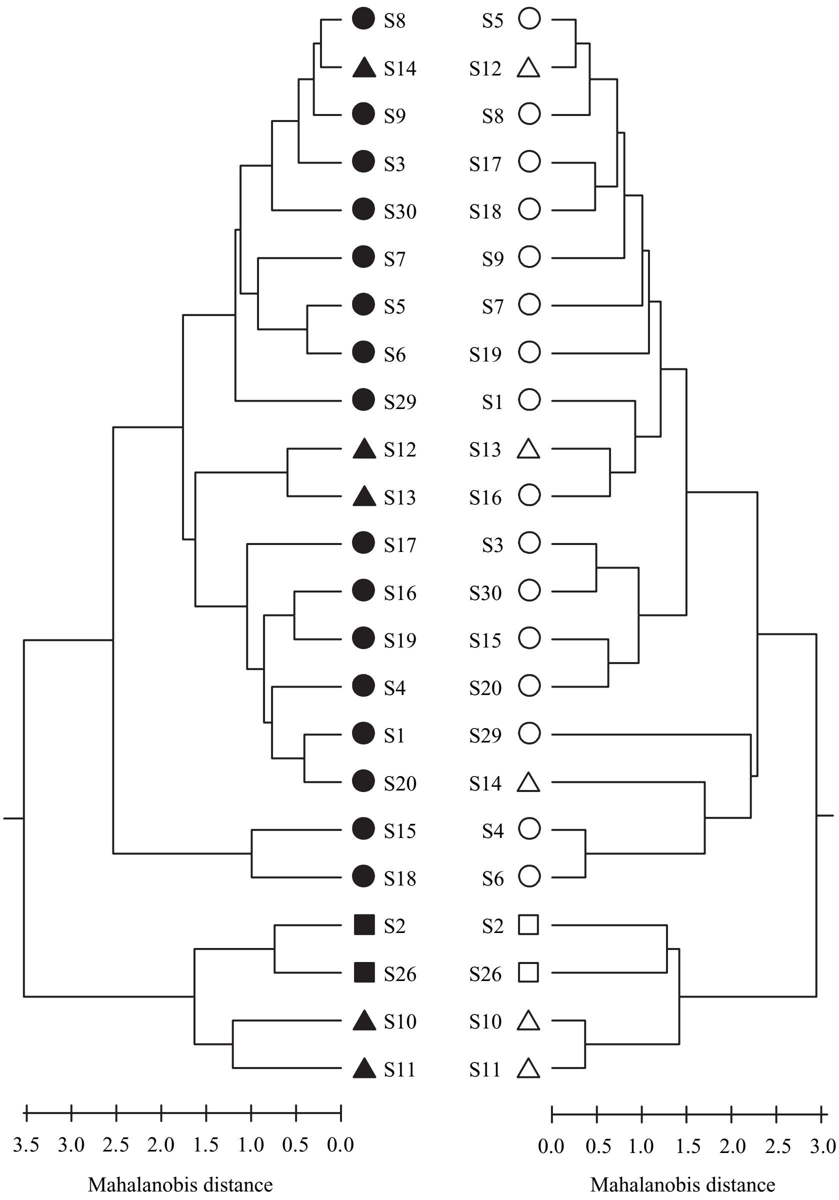

Figure 5. Phenograms for the 23 male (solid symbols) and female (empty symbols) sites of *G. atlantica* based on UPGMA cluster analysis of Mahalanobis D^2 distances. Site labels are as per Fig. 1.

assume that this is an ecological rather than a historical effect (see later), as they both survive in seemingly similar environmental conditions.

A recent mtDNA study (unpublished) by the authors has revealed that these morphotype groupings do not correspond to distinct maternal lineages and suggests that morphological differentiation is not due to ancient dispersal patterns or vicariance. Moreover, such effects would be expected to produce strongly concordant patterns between individual characters (Thorpe *et al*., 1991), which is not the case here. Rapid morphological differentiation through colonization of novel environments has been well documented in the literature (Orr & Smith, 1998; Reznick & Ghalambor, 2001). When patterns of morphological variation and environmental variation are closely associated, they are typically interpreted as evidence of local adaptations. However, there is increasing evidence that such patterns may contain an important non-genetic environmentally determined component. Rapid morphological differentiation due to adaptive phenotypic plasticity has been demonstrated in *Anolis* lizards (Losos *et al*., 2000, 2001). Whatever the cause, if the two isolated groups of *malpaís* populations do not have a common history, then they present a highly interesting model because they show parallel ecogenetic or environmental plasticity effects.

The assertion that *G. atlantica* from areas of Lanzarote associated with recent volcanic habitat attain adult body sizes greater than those from other parts of the island (López-Jurado & Mateo, 1992) is rejected by this study. The wider sampling regime used here reveals that male and female individuals of *G. atlantica* from areas not associated with recent volcanic habitat attain equal or often greater size. During fieldwork we were careful not to sample in *malpaís* areas visited regularly by tourists (such as the car park at Cueva de los Verdes) as we noticed that lizards were much more abundant and larger than at other *malpaís* sites (likely due to greater availability of organic matter). It is possible that sampling of these areas, where lizards were abundant, may have provided the source of bias for previous studies.

The trend for adult body size to be greater in the northern and southern regions of Lanzarote, and lower in the central region, is likely to reflect the intricate pattern of various genetic factors as well as proximate environmental and local population demographic factors. It is probable that an important component of the variation in adult body size documented here is attributable to variation in growth rates as a result of differences in food and water availability. The limiting effects of food and water availability on growth rates have been well established in several lizard species (Stamps & Tanaka, 1981; Guyer, 1988; Smith & Ballinger, 1994; Lorenzon *et al*., 1999).

However, the importance of food limitation on the pattern of size variation is difficult to assess based on the current data. It may also result from differential mortality such that lizards in the sparsely vegetated central region of Lanzarote have smaller adult body sizes because of shorter lifespans, on average. Despite the availability of several environmental explanations of the pattern of size variation, the possibility of an underlying genetic component cannot be ruled out. Substantial differences in growth rates documented in the eastern fence lizard *Sceloporus undulates* are known to have an important genetic component (Niewiarowski & Roosenburg, 1993).

The analyses of morphological variation of *G. atlantica* presented here allow evaluation of the subspecies classifications preferred by different authors. If these classifications are to be of any use, they should be predictive as well as useful for identification, and reflect primary patterns of geographical variation (Sneath & Sokal, 1973; Funk, 1982; Thorpe, 1982, 1987). Here, there are two clear morphological groupings that could be used as a basis for designating racial categories, similar to that generally accepted by recent authors (López-Jurado *et al.*, 1995).

The group comprising 17 of the 21 sites on the main island and those from the offshore islets corresponds to the widespread (*G. a. atlantica*) subspecies. Populations (S2 and S26) of *G. atlantica* studied from the north of Lanzarote correspond to ssp. *G. a. laurae* of the north-east of the island, which at present is only known from Malpaís de la Corona and areas to the south-east of Haría (Castroviejo *et al.*, 1985). The southern Timanfaya populations (S10 and S11) show closer morphological resemblance to those classified as *G. a. laurae* from north-eastern Lanzarote, but which are currently classified as *G. a. atlantica.* Thus the former subspecies category should include these two groups of geographically isolated populations.

However, before accepting and using these subspecies the subjectivity of such a proposal should also be considered. For example, the two populations from south Timanfaya and those from Malpaís de la Corona also seem to form consistent distinct phenetic groupings for males and females, as well as being geographically isolated from one another. Thus the designation of further taxonomic categories is also possible based on similar criteria used to define the two main morphological groupings.

In terms of the subspecies characteristics, *G. a. laurae* has been described as attaining considerably larger body sizes than *G. a. atlantica* (Castroviejo *et al.*, 1985; López-Jurado *et al.*, 1995). However, this is not found to be the case. Instead, *G. a. atlantica* from certain areas of Lanzarote is found to attain body sizes equal to or greater than those found for *G. a. laurae*.

Finally, although the within-island variation in morphology of *G. atlantica* is less pronounced than that found in several other lizard species on the adjacent islands of Gran Canaria and Tenerife (Thorpe & Báez, 1987; Thorpe & Brown, 1989; Brown & Thorpe, 1991; Thorpe, 1991; Brown, Thorpe & Báez, 1993), some interesting parallels are found. For example, there is some association between geographical patterns of morphological and environmental variation, which is generally found in lacertid and other lizards on the aforementioned islands. Also, there is a general tendency for the extent of population divergence to be related to the degree of environmental heterogeneity and/or age of potentially causal volcanic events. *G. atlantica* from Lanzarote fits this pattern, i.e. morphological divergence is relatively low, as is environmental variation, while quite extensive volcanic activity, which may have isolated populations, has been quite recent.

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APPENDIX

Sample details. Site names correspond to the most proximate town, village or landmark. Site labels and site symbols correspond to those given in Figure 1.

Site label	Island/islet	Year	Symbol	Site name
S1	Lanzarote	1999	●	Tías
S2	Lanzarote	1999	■	Punta del Palo
S3	Lanzarote	1999	●	Las Casitas de Femés
S4	Lanzarote	1999	●	Mala
S5	Lanzarote	1999	●	Costa Teguise
S6	Lanzarote	1999	●	Arrecife
S7	Lanzarote	1999	●	La Santa
S8	Lanzarote	1999	●	La Caleta de Famara
S9	Lanzarote	1999	●	Haría
S10	Lanzarote	1999	▲	El Mojón
S11	Lanzarote	1999	▲	Montaña de Halcones
S12	Lanzarote	1999	▲	Islote de Montaña Bermeja
S13	Lanzarote	1999	▲	Islotes de los Betancores (i)
S14	Lanzarote	1999	▲	Islotes de los Betancores (ii)
S15	Lanzarote	1999	●	Las Breñas
S16	Lanzarote	1999	●	Punta Pechiguera
S17	Lanzarote	1999	●	Yaiza
S18	Lanzarote	1999	●	Los Valles
S19	Lanzarote	1999	●	Vegas de Tegoyo
S26	Lanzarote	2002	■	Cueva de los Verdes
S29	Montaña Clara	1999	●	Entradero de Machín
S30	Alegranza	1999	●	Casas de Alegranza