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Testing multivariate patterns of within-island differentiation in *Podarcis dugesii* from Madeira

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Abstract

Podarcis dugesii is a polymorphic species found on the ecologically-heterogeneous Atlantic island of Madeira. Patterns of geographic variation in size-free body dimensions (body shape), scalation, and size were portrayed on maps with isophene contours. There was no dominant pattern of among-site variation as seen in several other island lizards, although some linear combinations of morphological variables showed evidence of clines towards the east coast. Multivariate statistical techniques were developed to evaluate whether morphological variation contained an ecology-related spatial pattern, after removal of the effects of statistical non-independence of studied populations. Specifically, a partial correlation matrix comparison method provided evidence to support a proposed elevation model of among-site divergence in scalation and body size, with both an alternative rainfall model and spatial non-independence held constant. Similar divergence in scalation has been observed in other lizard species on other island archipelagos as well on some continental areas. The rainfall model was rejected for both body shape and scalation. The degree of within-population polymorphism in body shape and scalation showed no clear geographic trends in general, although the elevation and rainfall models could not be rejected for female scalation.

Introduction

Clinal geographic variation in the morphologies of continuously-distributed animal species has frequently been explained as a selection-mediated response to

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present-day environmental variation (Endler, 1977). These conclusions are usually based on environment-morphology correlations. The discovery of a significant correlation often leads to hypotheses concerning potential underlying ecogenetic causes, particularly where there appears to be some obvious functional relationship between the variables measured (e.g., Douglas and Endler, 1982; Daltry et al., 1996).

Clearly there are problems with this approach, not least because an *a posteriori* search for potentially important environmental gradients will on average lead to one significant 'nonsense' correlation for every twenty (independent) patterns tested, misleading the researcher into considering inappropriate underlying mechanisms of differential selection. Despite this, studies of within-island microgeographic variation in lizards are beginning to show broadly consistent results in support of the *in situ* ecogenesis theory. Seven species of lizard (from four lizard lineages) show patterns of morphological population differentiation on two island archipelagos (the Canary Islands and the Lesser Antilles) which correspond very closely to aspects of the thermal environment and/or habitat humidity. The variation does not appear to result from superficial environment-phenotype interaction because mtDNA (Malhotra and Thorpe, 1994) and allozyme variation (Mayer and Tiedemann, 1991), concordant with the morphological differentiation, were found in two species additionally subjected to biochemical studies. Further support for the theory of between-habitat selection differentials was provided by a transplant experiment (Malhotra and Thorpe, 1991a).

Although this evidence appears convincing, recent studies indicate that present-day selection gradients may not completely account for the observed patterns. The categorical nature of some of the microgeographic patterns, and the magnitude of the sequence divergence between mtDNA haplotypes suggests that historical population vicariance may have also contributed, at least in some cases (Brown and Thorpe, 1991a, b; Thorpe et al., 1994; Pestano and Brown, unpubl. data).

This report deals with microgeographic variation in a lizard on an island for which explicit hypotheses of population differentiation have not previously been tested. *Podarcis dugesii* is known to show considerable morphological variation both within-sites and within- and among islands of the Madeiran archipelago (33° N, 17° W) (Cook, 1979; Davenport and Dellinger, 1995). Madeira itself is the largest and most ecologically heterogeneous island because of its altitude (1861 m) and topography and shows marked differences in rainfall and temperature between different areas. *P. dugesii* therefore provides an ideal model for numerical hypothesis testing of ecogenetic responses to changes in habitat humidity and the thermal environment. This is achieved using novel statistical methods which represent refinements of some existing techniques for studying geographic variation.

Materials and methods

Specimens, sites and characters

Podarcis dugesii (335 males, 330 females) were trapped at 32 evenly-distributed sites within the island of Madeira (Fig. 1). Although this species is generally

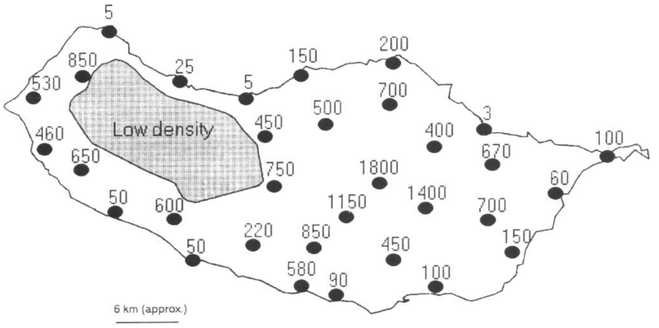


Fig. 1. Positions and elevations (m) of sample sites within Madeira.

extremely abundant, a large area of absence/low density was identified in the high elevation area in the west of Madeira. Specimens were fixed with formaldehyde and preserved in alcohol. The following seven linear body dimensions were recorded (from the right hand size where appropriate) of each lizard: snout-vent length, head length – measured dorsally, head width, fore limb length, hind limb length, foot length, snout to shoulder distance. Six scalation characters were also recorded: gular scales (G), collar scales (C), dorsal scales (D), ventral scales (V), femoral pores on hind limb (FP), infra-digital lamellae on the fourth toe of the rear limb (IDL).

Patterns of among-site variation

This study aimed to detect general trends within different aspects of the morphology rather than attempting to relate (non-independent) characters to potentially causal environmental gradients. Emphasis was therefore placed on obtaining and analysing independent linear combinations of characters. Males and females were separated for the analyses.

Orthogonal components representing among-site variation in body shape were computed by first sweeping the effect of an *a priori* defined isometric size vector from the body dimensions and then computing canonical variates analyses (CVA) on the adjusted values. This method of size-removal followed a suggestion made by Rohlf and Bookstein (p. 362, 1987) based on methods presented by previous researchers (Jolicoeur, 1963; Burnaby, 1966; Somers, 1986). The direction cosines of the first principal component of a principal components analysis on the covariance matrix of the p log-transformed body dimensions are ($p^{-0.5}$, $p^{-0.5}$, $p^{-0.5}$, $p^{-0.5}$, $p^{-0.5}$, $p^{-0.5}$, $p^{-0.5}$), if it represents isometric size (Jolicoeur, 1963). This was represented as a column vector, F_1. Male and female scores on this vector were obtained by multiplying the log-transformed data matrix by F_1. Its effects were then removed from the body dimensions using Burnaby's method (1966). This involved computing an idempotent p by p symmetric matrix, L, as

$$L = I_p - F_1(F_1'F_1)^{-1}F_1'$$

(where F_1' is the transpose of F_1 and I_p is a $p \times p$ identity matrix) which was then premultiplied by the log-transformed data to obtain a completely (isometric) size-free body shape matrix. CVAs summarised among-site variation in male and female body shape.

Site mean canonical variate scores (CV) for axes expressing non-trivial proportions of among-site variation were plotted on maps with contours spaced at intervals of 1 S.E. (based on pooled within-group standard deviations) in order to aid visualisation of any geographic trends (Golden Software, 1990). This is viewed as purely an exploratory data method aimed at providing an initial indication of broad trends prior to more rigorous statistical hypothesis testing.

A previous study has described considerable within-site polymorphism in colour pattern and body dimensions of this species (Davenport and Dellinger, 1995) so overall (multivariate) variability in body shape at each site was estimated as Mahalanobis D^2 distances between individuals and group centroids. The mean D^2 distance at each site therefore estimates the degree of generalised within-population polymorphism. Mean variability was plotted in the same way to that described for mean canonical scores.

CVAs were used to summarise among-site variation in scalation. Plotting of means and contouring was used to portray geographical trends. Within-population polymorphism in scalation was evaluated and portrayed in the same way to that described for body shape.

The degree of congruence in the patterns of among-site differentiation between males and females and between character systems was assessed by computing correlation coefficients between matrices (multivariate comparisons: body shape and scalation) or group means (body size). Significance was assessed using randomisation (multivariate comparisons) or the probability density function of r under the null hypothesis. It should be remembered that a significant correlation is merely indicative of the presence of a (linear) bivariate relationship: in this case interest is primarily focused on the degree of congruence which is assessed from the magnitude of r and not through hypothesis testing.

Testing ecogenetic hypotheses of geographic variation in morphology

Putative causes can be modelled in terms of the spatial patterns that they predict, and so can be evaluated by statistical comparisons with observed patterns. Although new methodology for performing phylogenetically-independent analyses has recently been the subject of a considerable amount of interest, there have been relatively few developments of statistical techniques for making intraspecific comparisons among contiguous populations, i.e., removal of gene-flow mediated non-independence of sample-sites: comparisons across contiguous populations must allow for spatial autocorrelation arising through gene flow.

The nature of the functional relationship between morphological divergence and geographic distance must be known if independence of sample sites is to be achieved. Theoretically, this requires an *a priori* model based on extensive field data. Despite this difficulty, exploratory data analyses indicated that a linear model provided a good approximation that was superior to the other simple alternatives that were tested. This geographical proximity model took into account the very low population densities/absence of *P. dugesii* found in the high plain in the centre/north-west of the island, by assuming that gene-flow approximated to zero over this area, and was formulated as a between-site distance half matrix of dissimilarities.

Patterns of geographic variation in other lizard species have frequently been found to be related to some proxy of habitat humidity, such as total annual rainfall or degree of vegetation luxuriance (Thorpe and Brown, 1989; Brown et al., 1991; Malhotra and Thorpe, 1991b). Elevation also appears to be important for some species/characters (Brown and Thorpe, 1991a), the effects of which may be assumed to act through changes in the thermal environment if it is independent from habitat humidity (or has been statistically modelled in such a way that humidity is held constant). The two main components of the environmental variation in Madeira are temperature and rainfall. Elevation and ranked total annual rainfall models were therefore formulated as distance half-matrices based on linear differences between sites.

Observed half matrices comprised the Mahalanobis D^2 distances between group centroids for body shape, scalation, and the between-site differences in mean size, for males and females. Evaluation of hypotheses required estimation of the strength of the relationship between the morphology and the ecogeography matrices. Although Manly's multiple regression extension of the Mantel test has been quite widely-used to compare biological matrices with various models simultaneously (Manly, 1986; Brown et al., 1991; Thorpe and Báez, 1993; Daltry et al., 1996), it would appear more appropriate to measure the strength of the relationship between the variables using a correlation-based test, rather than computing partial regression coefficients. Sokal et al. (1991) used a partial correlation approach to test single models of population expansion against genetic distances with geographic distances held constant. Here, we extend this to obtain second-order partial correlations that allow proximity and one other ecogeography matrix to be held constant when assessing the relationship between observed and ecogeography matrices. This represented an important step in extricating the two ecological effects because rainfall tends to be higher on the north-facing slopes of Madeira and also increases with elevation. Non-independence/non-normality of the matrix elements meant that a matrix randomisation procedure was required to determine significance. This method was written by one of the authors (RPB) and essentially represents a partial correlation extension of Mantel's test (Mantel, 1967).

Second order partial correlations were computed between 1) the observed and the rainfall matrices with proximity and elevation held constant, and 2) the observed and the elevation matrices with proximity and rainfall held constant. Significance

Table 1. Congruence in patterns of among-site variation between body shape, scalation, and size (males, lower off-diagonal elements; females, upper off-diagonal elements) and between males and females (diagonal elements) as assessed by product-moment correlation coefficients (r) between matrices with probabilities obtained under randomisation (5000 permutations) or between vectors using the probability density function of the correlation coefficient (for male vs. female body size).

	Body shape	Scalation	Body size
Body shape	$r = 0.183$, $P < 0.0002$	$r = 0.224$, $P < 0.0002$	$r = 0.348$, $P < 0.0002$
Scalation	$r = 0.094$, $P = 0.0162$	$r = 0.151$, $P < 0.0002$	$r = 0.280$, $P < 0.0002$
Body size	$r = 0.120$, $P = 0.0058$	$r = -0.063$, $P = 0.9200$	$r_{[30]} = 0.823$, $P < 0.0001$

was determined as the proportion of partial correlations that were greater than or equal to the observed partial correlation after 4999 randomisations of the observed distance matrix (the observed ordering of the data is included as one of the possible data orderings so the maximum level of significance that can be achieved is 0.0002). This constituted a one-tail test because the alternative hypothesis specified that the extent of morphological divergence should be positively related to the magnitude of the ecological difference between the sites.

Twenty P-values are presented so comparison with standard significance levels may lead to spurious rejection of null hypotheses for some of the ecology-morphology comparisons. Bonferroni/Dunn-Šidák corrections can be made which adjust significance levels to take this into account (e.g., Rice, 1989 and references therein), however this tends to be conducive to attaching too much importance to the chosen level, rather than enhancing the superior view that the P-value merely reflects the weight of the evidence against the null hypothesis. This point is especially important when considering the results of randomisation tests (and even more so when the number of randomisations computed is low), because the P-value represents only an estimate of the true P-value based on a random sample of data reorderings. For this reason, hypotheses will not be rejected out of hand simply because they do not meet a specified significance level.

Results

Patterns of geographic variation

The correlation between male and female patterns of among-site divergence in body dimensions (although significant) was low indicating that the level of congruence was not high (Tab. 1). Generalised geographic variation in male and female body shape was complex, i.e., comprising several different patterns. Canonical vectors (CV) 1, 2 and 3 expressed 34.8%, 24.4%, and 16.0% (males) and 43.4%, 19.5%, and 13.7% (females) of the among-site variation, respectively. Maps of CV scores provided evidence of a cline between the east coast and the centre of the island for male CV1 and female CV2 and CV3 (Figs. 2a, 2c, 2d), and tentative evidence of similarity among mid-high elevation populations in the centre of the island for male CV2 (Fig. 2b). Geographic variation in other components was largely mosaic, i.e., no strong tendencies for either gradual changes with increasing separation or similarity among groups of geographically-proximate sites.

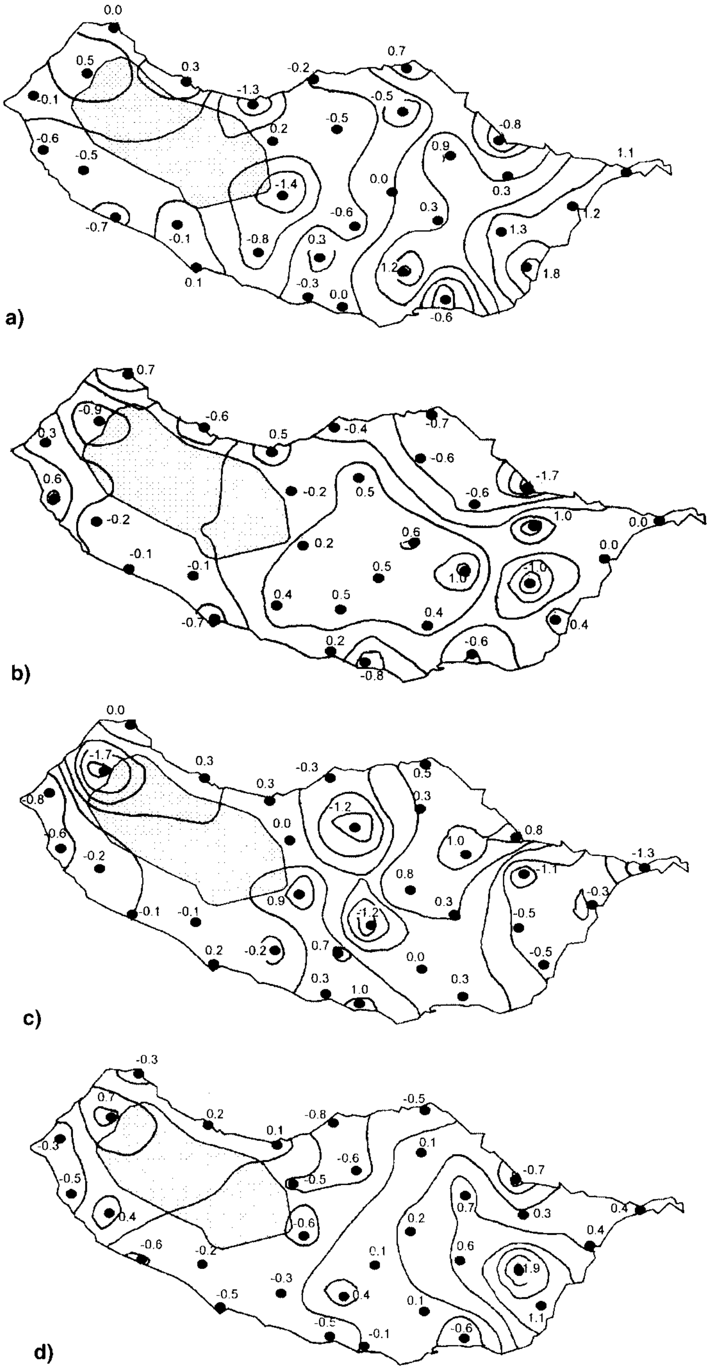
Patterns of geographic variation in mean size were highly congruent between males and females (Tab. 1). Largest lizards occurred at two proximate high elevation sites in the east of the island, and smallest lizards either on the extreme east coast (females – Fig. 2e) or the north coast (males). There were no clear patterns of among-site variation in overall variability in male and female body shape.

Pooled within-site correlations between pairs of scalation characters were generally positive and low indicating that they represented reasonably independent components of the phenotype. The highest correlations were between IDL and FP (males, $r = 0.32$; females, $r = 0.24$), between IDL and G (males, $r = 0.19$; females, $r = 0.26$), between G and D (males, $r = 0.24$; females, $r = 0.17$), between G and FP (males, $r = 0.20$; females, $r = 0.22$), and between FP and D (males, $r = 0.19$; females, $r = 0.22$). All other pair-wise correlations were between -0.098 and 0.163.

Congruence between male and female among-site divergence in scalation was low, but significant. Variation in phenotypically-independent components of scalation were complex: CVAs were unable to greatly reduce the number of dimensions in the among-site variation. The first four vectors expressed 28.9%, 23.4%, 19.2% and 14.2% of the among-site variation in male scalation, and 30.6%, 21.6%, 17.6%, and 15.9% of the variation in female scalation. Contour maps did not reveal any clear trends, although there was a weak tendency for differences between sea-level coastal and high elevation inland populations for male CV1 (Fig. 2f). This CV contrasted increasing ventral scales/femoral pores with decreasing dorsal scales/infra-digital lamellae. Among-site variation in overall variability in male and female scalation was largely mosaic (i.e., no obvious geographic trends).

Hypothesis testing

Second order correlation coefficients with probability estimates obtained under randomisation are presented in Table 2. There is evidence to support the elevation model for both scalation and the body size vector, once the effects of geographic proximity and rainfall have been partialled out. Evidence for a strong relationship between scalation and elevation is further substantiated by the parallel results obtained for males and females. The partial correlation between female size and rainfall is also highly significant. None of the models appear to explain patterns of geographic variation in body shape (males and females) or degree of within-population polymorphism in body shape for either males or females. A significant relationship was found between levels of polymorphism in female scalation and elevation and also rainfall differences between sites, although no such relationships were found for males.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b)
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d)
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Fig. 2.

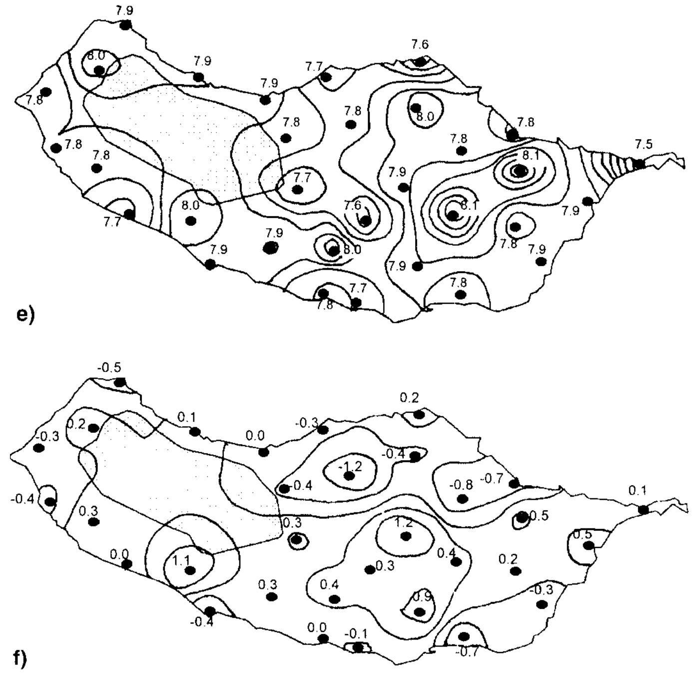

Fig. 2. Patterns of microgeographic variation in CVA scores: a) male body shape, CV1, b) male body shape, CV2, c) female body shape, CV2, d) female body shape, CV3, e) female body size, f) male scalation, CV1. Contours are spaced at one pooled within-group S.E. of the means.

Discussion

Numerous surveys of geographic variation in mtDNA, allozyme, and morphology on a wide range of taxa have revealed several broad patterns. Many species, particularly in the southern U.S., follow a pattern in which population differentiation is concordant with present-day spatial discontinuities (Avise et al., 1983; reviewed in Avise et al., 1987). Other studies have revealed phylogeographic distributions in continuously-distributed species which are concordant with putative historical vicariance (e.g., Thorpe, 1984 [snakes]; Bermingham and Avise, 1986 [freshwater fish]; Lamb and Avise, 1992 [freshwater turtles]; Gallant et al., 1993 [invertebrates]). When no such scenario seems likely and the geographic variation is still concordant with an environmental gradient after removal of the effects of spatial autocorrelation then selection-moulded differentiation may appear to be the most plausible explanation. Such findings have occasionally been lent even greater support by the discovery of parallel patterns between two sympatric or allopatric species (Endler, 1982; Anderson and Oakshott, 1984; Romano et al., 1987; McDonald and Siebenaller, 1989; Brown et al., 1991).

Within-island geographic variation in lizards is extremely useful to the evolutionary biologist in this respect. The fact that substantial variation is found in species

Table 2. Partial correlation Mantel tests of morphology distance matrices (M) with rainfall and elevation models of differentiation, with geographical proximity (G) and either elevation (E) ($r_{\mathrm{MR.GE}}$) or rainfall (R) ($r_{\mathrm{ME.GR}}$) held constant. Body shape and scalation matrices are based on Mahalanobis D^2 distances between group centroids, the size matrix is based on the mean group score for the isometric size vector, and the polymorphism distances are based on mean within-group Mahalanobis D^2 distances from the group centroids. Probability estimates (P) were obtained from 5000 matrix permutations (see Materials and methods). Note that when the true probability is 0.05, then 99% of probability estimates are expected to fall within the limits (0.042, 0.058), corresponding values for a true probability of 0.01 are (0.006, 0.014).

		Elevation		Rainfall	
		$r_{\mathrm{ME.GR}}$	P	$r_{\mathrm{MR.GE}}$	P
Body shape:	male	−0.010	0.5806	0.042	0.1722
	female	−0.075	0.9520	0.053	0.1188
Scalation:	male	0.234	0.0002**	−0.070	0.9438
	female	0.071	0.0570*	−0.098	0.9836
Size:	male	0.066	0.0760*	0.019	0.3386
	female	0.079	0.0410*	0.189	0.0002**
Body shape polymorphism:	Male	−0.059	0.8982	−0.127	0.9988
	female	0.033	0.2216	−0.095	0.9854
Scalation polymorphism:	male	0.053	0.1238	−0.005	0.5460
	female	0.110	0.0082**	0.141	0.0010**

* Some evidence (albeit quite weak) against the null hypothesis of no partial correlation (H_0).

** Strong evidence against H_0.

found within limited geographical areas allows a comprehensive description of the spatial pattern, facilitating explication of cause. Comparisons between islands to arrive at a general thesis is also possible because many show broadly similar patterns of ecological heterogeneity.

Assessment of the patterns of geographic variation in mean morphology of *P. dugesii* indicates that large-scale population vicariance has not played an important role in determining the observed pattern of geographic variation. Categorical variation might be expected if secondary contact between long-term vicariant populations had occurred but evidence of this is not seen in any of the canonical variates. Also, the patterns are not strongly concordant among characters which tends to be the case when either historical dispersal patterns or vicariance are the cause (Thorpe et al., 1991; Sokal and Wartenburg, 1983; but see Eastel, 1989 and Sokal et al., 1991).

Even so, certain aspects of the variation are difficult to explain in terms of current ecological heterogeneity and it is worthwhile pointing out that the eastern clines in male and female body dimensions show some concordance with a scenario based on a known geological event in the island's history. The island was formed by volcanic eruptions approximately 20 Ma. During more recent times (less than 1 Ma) a north-south ridge was formed by volcanic action, temporarily separating the eastern peninsula (represented by the two most easterly sample site in this study) from the rest of the island which may have caused some localised vicariance. Even more recently (about 18000 years ago) Madeira appears to have been connected by this same peninsula to the small Deserta islands during a period of (at most) a few thousand years so intergradation could have occurred if *P. dugesii* was already present on the Desertas when this landbridge was established. Both of these events have been implicated in the evolution of land snails on Madeira (Cook et al., 1990; Cameron and Cook, 1992).

The presence of rainfall-independent elevation-related variation in scalation is indicative of a temperature-mediated response. This type of variation has now been described in the scalation of the lacertid lizard *Gallotia galloti* on the island of Tenerife (Canary Islands) (Thorpe and Báez, 1987), as well as the scincid lizard *Chalcides sexlineatus* (Brown and Thorpe, 1991a) and to a lesser extent *Gallotia stehlini* on Gran Canaria (Thorpe and Báez, 1993) and *Anolis oculatus* in the Caribbean island of Dominica (Malhotra and Thorpe, 1991b). Other species have not been studied at such a wide elevational range and so comparisons may be misleading because the absolute character change may be too small to identify it as an elevational response.

Previous researchers have described geographic variation in the number of body scales in lizards and subsequently inferred that they reflect adaptive responses to variation in rates of either water-loss or heat-loss via their influence on surface area (Soulé, 1966; Horton, 1970; Soulé and Kerfoot, 1972; Thorpe and Báez, 1987; Brown and Thorpe, 1991a). The former explanation has been put forward for some species, while the latter appears more appropriate for others. Clearly cross-species comparisons must be made within an explicit phylogenetic framework in order that a general thesis on adaptive responses be obtained (Harvey and Pagel, 1991). However, the methods used here separate rainfall and elevation effects and indicate that scalation in *P. dugesii* responds solely to variation in the thermal environment, mirroring the situation in another lacertid lizard (*Gallotia galloti*) that is subject to substantial temperature and humidity variation among habitats within the island of Tenerife (Thorpe and Báez, 1987). Whatever the exact environmental factors that give rise to the differing patterns of directional selection on scalation, the evidence clearly supports the theory that differentiation is ecogenetic in origin.

Mean body size is greatest at higher elevation sites and tends to be lower at some of the coastal sites, reflecting patterns seen in some lizard species (e.g., Malhotra and Thorpe, 1991b) although showing the opposite trend to that described in others (e.g., Thorpe and Brown, 1991). This variation is likely to reflect various (interacting) environmental and genetic factors which cannot be disintricated on the basis of the current data. Even so, it could be expected that growth rate differences represent an important component of body size variation. Very substantial differences in growth rates have been described for *Sceloporus* lizards in the U.S. (e.g., Tinkle and Dunham, 1972) which appears to have a genetic basis (Ferguson and Brockman, 1980; Niewiarowski, 1995). If a similar growth-rate argument is invoked to explain the tendency for larger body size at high altitudes in *P. dugesii* then the differences must be considerable to overcome the thermal-constraints that should reduce annual growth rates at high altitude.

Acknowledgements

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