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Microgeographic variation in the colour pattern of the lizard *Gallotia galloti* within the island of Tenerife: distribution, pattern and hypothesis testing

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This study of the microgeographic variation in the colour pattern of the lizard, *Gallotia galloti*, within Tenerife has three facets. One, an analysis of the population distribution and density in relation to physical conditions; two, univariate and multivariate descriptions of the pattern of geographic variation; and three, formal testing of a range of causal hypotheses for these geographic patterns. The range is not divided into separate allopatric high- and low-altitude populations by a mid-altitude ring of ground-level cloud although there is a drop in population-density in the middle altitudes. Multiple regression indicates that, of the factors measured, this is primarily due to a decrease in insolation. The pattern of geographic variation in the six independent colour pattern characters is portrayed by contouring the 67 locality means. There is generally good congruence among these patterns and a canonical analysis indicates that the generalized pattern of geographic variation is largely unidimensional and can therefore be represented adequately by (and portrayed by contouring) the first canonical variate. Seven causal hypotheses, from a range of possible and previously suggested causes, are considered. The procedure for testing these hypotheses should depend on their dimensionality and that of the observed pattern. Since all the observed and hypothesized patterns are basically unidimensional the seven hypothesized patterns were simultaneously tested against each observed pattern (individual characters and canonical variate) by partial correlation. All the previously suggested 'phylogenetic' hypotheses based on divergence in allopatry are rejected. The hypotheses that the geographic variation in the colour pattern is caused by the topographically determined climate cannot be rejected. The character state changes can be explained by a balance between sexual selection for 'attractive' colouration and natural selection, via predation, for cryptic colouration.

KEY WORDS: Microgeographic variation – hypothesis testing – colour pattern – crypsis – sexual selection – lizards.

CONTENTS

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INTRODUCTION

The medium-sized vegetarian lizard, *Gallotia galloti*, is found on the western Canary Islands and shows, like so many other island species, inter-island geographic variation (Thorpe, 1985a). One of the reasons for the popularity of the study of inter-island evolution is that islands are assumed to be conveniently discrete, homogeneous units. Notwithstanding this assumption, research has shown microgeographic variation of this species within the island of Tenerife in a wide range of features. Bischoff (1982) divided the Tenerife population into northern and southern subspecies largely on the basis of the colour pattern, without using unit characters. Bischoff suggested that a possible cause of this variation is secondary meeting of forms from the two ancient precursor islands of Anaga and Teno when these islands were fused by the eruption of Teide between them. Thorpe & Baez (1987) carried out a detailed multivariate study of the microgeographic variation in the scalation and body dimensions of *G. galloti* in Tenerife and revealed a mix of WNW-ESE clines in body dimensions and latitudinal and altitudinal clines in scalation, with ecological adaptation being implicated as the cause in at least the latter case. Also, Pasteur & Salvidio (1985) have suggested that, based on isozyme differences at four localities, high-altitude populations and low-altitude populations are separated by a zone of ground-level cloud encircling the islands in the middle altitudes.

Of the various features of this Tenerife population that show microgeographic variation, the colour pattern of sexually mature males is the most striking. Some adult males have a largely uniform black/brown dorsal surface, whilst others have a strong pattern of yellow cross bars; some have bright blue cheeks whilst others have blue blotches on the trunk. The aim of this study is to test various hypotheses regarding the cause of this variation. Before doing this, it is necessary to reveal the pattern of distribution and population density and to describe the pattern of microgeographic variation in quantitative terms.

DISTRIBUTION AND DENSITY

The island of Tenerife is 2058 km^2 in area and 3718 m at its highest point. There are substantial differences in climate within this island; the low altitude north-facing slopes are warm, humid and cloudy whilst elsewhere it can be hot and arid. There is also distinct altitudinal zonation due to a ground-level cloud layer in the middle altitudes, which gives cool humid conditions, especially in the north. Above the cloud layer it can be hot and arid, although at the highest altitudes of Mount Teide it is cooler (Thorne & Baez, 1987). Diurnal and seasonal rhythms are also more pronounced at higher altitudes.

This species is heliothermic (Baez, 1985; unpublished observations) and its distribution and density may be related to climate conditions which may in turn determine the level of gene flow among populations. This is pertinent to the hypothesized cause of geographic variation in this species on Tenerife (Pasteur & Salvidio, 1985), as the level of microgeographic or local differentiation within a species may reflect the relative influence of gene flow and the physical,

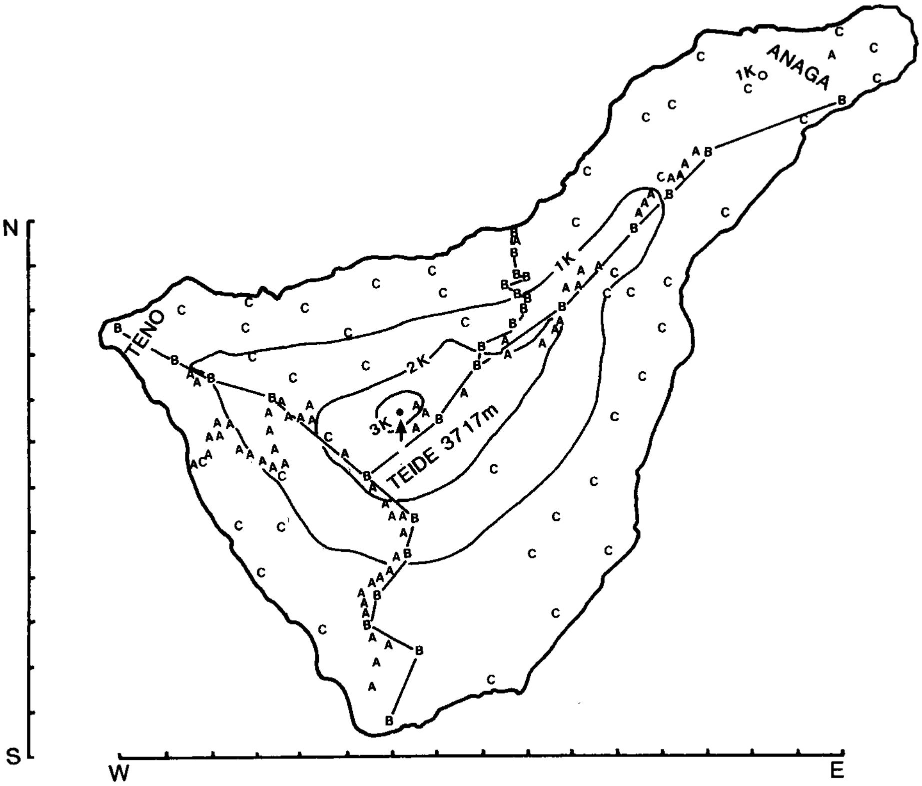

Figure 1. Map of Tenerife indicating the various types of locality (A,B,C). At type A localities only the presence of lizards was recorded; at type B localities presence, population density and colour pattern were recorded; and at type C localities both presence and colour pattern were recorded. Consequently, presence or absence of lizards was recorded at all types of locality (A, B and C); population density was studied at locality type B (joined by lines and projected against transects NS and EW for Fig. 2); and the colour pattern was studied at locality types B and C). The contours at 1000 m (1K), 2000 m (2K) and 3000 m (3K) are given.

ecological, ethnological and genetic factors that restrict it (Anderson, 1970; Endler, 1979; Handel, 1982, 1983; Handel & Le Vie Mishkin, 1984; McCauley, 1983; McNeilly & Antonovics, 1967; Pamilo, 1983: Patton & Feder, 1981; Varvio-Aho & Pamilio, 1980). In light of the suggestion that lizards are absent from the middle altitudes (Pasteur & Salvidio, 1985) it is necessary to determine what factors influence population density, the pattern of distribution and population density, and whether or not there is a high-altitude population which is allopatric to a low-altitude population.

Density—methods

To determine their distribution, lizards were scored as present or absent from a series of localities throughout the island (localities of type A, B and C, Fig. 1) during July and August 1986 and 1987. In particular, the reported areas of absence on the middle altitude slopes were investigated at 100 m altitudinal intervals.

Population density was investigated at type B localities (which are arranged in approximate longitudinal and latitudinal transects, Fig. 1), plus a few others. The choice of localities was influenced by the accessibility of the terrain. A simple estimate of relative population density for localities, outside the Canadas National Park, was recorded as the number of lizards per trap hour (using tomato-baited traps set for 30 minutes around midday).

At the same time as the trapping exercise the relative humidity, relative insolation and shade temperature were recorded from these (type B) localities. The relative isolation was recorded as the light reflected from a standard surface with values coded on a 0 (Min.) to 10 (Max.) scale. The relationship between relative density cloud cover, tree cover, altitude, temperature, relative humidity and relative insolation was investigated by simultaneously plotting these factors against the latitudinal and longitudinal transects. The relationship between the quantitative variables was investigated using partial correlation analysis with relative density as the dependent variable and relative humidity, relative insolation and temperatures as the independent variables.

Density—results and conclusions

The investigation of localities A+B+C (Fig. 1), revealed that lizards were present on all the middle altitude slopes (north, south, east and west) at altitudinal intervals of 100 m or less with the exception of one locality on the northern slope and even there faeces of *G. galloti* were present. There is no substantial contiguous band of territory around the middle altitudes from which lizards are absent. Population density varies but *G. galloti* appears to be found practically everywhere that vegetation occurs, that is, up to *c.* 2800 m altitude in this study 3200 m according to Klemmer (1976). The longitudinal and latitudinal transects (Fig. 2) show that population density is high at low and high altitudes (excluding the very highest altitudes of Teide), but drops at middle altitudes coincident with the ring of ground-level cloud. This ground-level cloud cover and the related drop in relative population density is particularly pronounced on the northern and eastern transects. Note, however, that a zero recording for relative population density along these transects does not indicate the absence of lizards, only that none was trapped in the given time. The relative density is significantly positively correlated with relative insolation and significantly negatively correlated with relative humidity. However, partial correlation indicates that of the three variables (temperature, insolation and humidity), insolation is the primary factor influencing the relative population

TABLE 1. Correlation and partial correlation between relative population density and the ecological variables (temperature, relative humdity and insolation)

	Correlation	Partial correlation
Temperature	0.416	−0.227
Relative humidity	*−0.712	−0.292
Relative insolation	*0.757	*0.493

*$P < 0.05$.

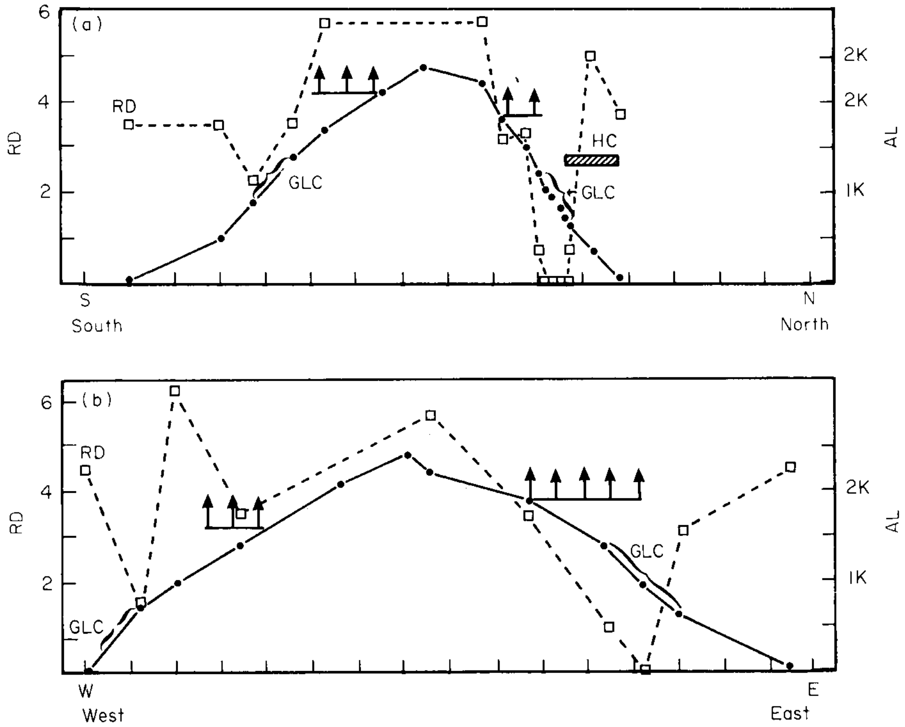

Figure 2. Latitudinal (2a) and longitudinal (2b) transects based on type B localities projected against line and EW (Fig. 1) respectively. The altitude (AL) of the type B localities is given in thousands of metres and the distribution of coniferous trees is indicated by vertical arrows. The relative population density (RD) is given in lizards-per-trap-hour, and there is an indication of the distribution of high cloud (HC), and ground-level cloud (GLC) at the time the population density was recorded. Note that a zero recording for relative population density does not indicate a complete absence of lizards.

density (Table 1). This is compatible with the heliothermic mode of thermoregulation in this species (Baez, 1985).

It is apparent that, although there are two bands of relatively high population density around the island (at altitudes lower and higher than the ground-level cloud), these two bands are not allopatric, i.e. separated by a ring of terrain devoid of lizards, *sensu* Pasteur & Salvidio (1985). However, the middle altitude ring of ground-level cloud does result in a ring of terrain with low insolation where the population density is reduced, albeit slightly on the southern slopes (Figs 2, 3).

PATTERN OF MICROGEOGRAPHIC VARIATION

A quantitative description of the pattern of geographic variation is an essential prerequisite for any worthwhile discussion of the cause of the variation, for testing specific hypotheses and for any worthwhile consideration of trinomial nomenclature. Whilst the variation in individual characters is of central interest in this study, it is also important to consider a multivariate generalization of the geographic variation in the colour pattern (Thorpe, 1976, 1983, 1987a).

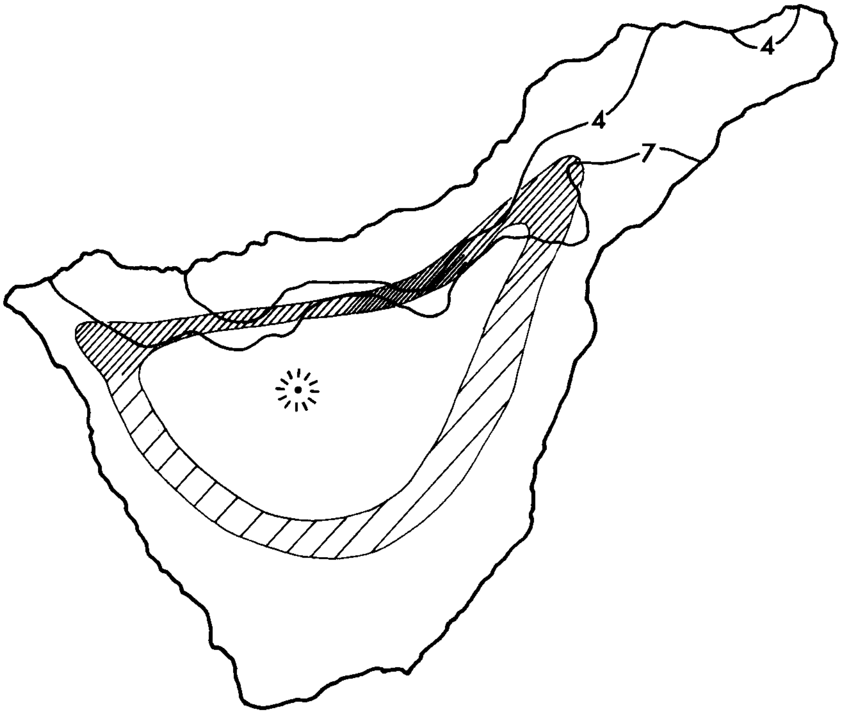

Figure 3. Approximate distribution of the areas of relatively low population density coincident with the ring of ground-level cloud (oblique hatching). The transition zone between the colour pattern forms is represented by the area between the 4th and 7th contours of the first canonical variate scores (based on locality means on a 0 to 10 scale).

Pattern—methods

The investigation of the colour pattern encompassed 501 sexually mature males (in full breeding colour) from 67 localities. These localities (type B and C. Fig. 1) were dispersed throughout the island to represent all geographic positions.

The following characters were recorded from high quality photographs:— (1) the number of yellow bars between the limbs covering two or more scales; (2) the number of blue dorsolateral blotches from shoulder to hind limb; (3) the mid-point depth of the first two major blue dorsolateral blotches counted in scales; (4) the number of scales covered by the yellow dorsal bar above the shoulder; (5) the depth of the blue chin marking from the ear along the supralabials counted in scales; and (6) the minimum number of dorsal scales separating the first two major blue dorsolateral blotches. The highest value and lowest value for a locality mean, together with the pooled within-locality standard deviation, is given for each character in Table 2.

The existence of significant among-locality variation was assessed by a one-way ANOVA with each locality representing a group. The pooled within-locality product-moment correlation was computed between colour pattern characters to indicate the extent to which they are independent characters, *sensu* Thorpe (1976, 1987a). The among-locality correlation was computed between

TABLE 2. Summary statistics for the colour pattern characters

	Minimum locality mean	Maximum locality mean	Pooled with-locality standard deviation
Char. 1	2.25	11.50	1.80
Char. 2	3.80	8.33	1.70
Char. 3	11.50	34.50	5.59
Char. 4	0.00	15.60	3.03
Char. 5	0.00	6.29	1.51
Char. 6	0.00	14.00	2.62

characters using the mean character state per locality. This indicates the congruence in their patterns of geographic variation.

Canonical variate analysis (CVA) of the six colour pattern characters across the 67 localities was used to depict generalized trends in the geographic variation of these characters because it takes into account the within-group covariance between them. This was checked by a principal component/coordinate analysis (PCA) on the mean character states for each of the 67 localities. PCA, unlike CVA, does not assume homoscedasticity of the within-locality covariance matrices. Although the later analyses are based on CVA scores, the first canonical variate and first principal component are effectively identical (locality mean scores correlated at $r = 1.0$), so one can consider them as interchangeable for the purposes of this study. Multiple group principal component analysis (MGPCA) was also run on these six characters across the 67 localities in order to detect within-locality constellations of inter-dependent characters (Thorpe, 1983, 1988 and references therein).

The pattern of geographic variation in the individual characters is defined by the distribution of locality means in geographic space. The generalized pattern of geographic variation in the colour pattern is defined by the locality mean scores along the first canonical variate (CVI), or first principal component (PCI), whilst geographic variation in the within-locality character constellations is defined by the locality means of the MGPCA scores. Where appropriate, these patterns of geographic variation are illustrated by isophene contours on a 0 (Min.) to 10 (Max.) scale produced by the Surface II program (Sampson, 1978).

Pattern—results and conclusions

All six characters showed significant ($P < 0.001$) among-locality variation (ANOVA) and were consequently used for all subsequent analyses. The among-locality correlations are generally high (Table 3) indicating congruence between the patterns of geographic variation, whilst the pooled within-locality correlations are generally low (Table 4) indicating that the characters represent independent facets of the phenotype (Thorpe, 1976). The MGPCA also indicated that there are no constellations of within-locality correlated characters. Consequently, the use of MGPCA was pursued no further in this study.

The isophene contours for the six individual characters (Fig. 4A–F) illustrate the patterns of geographic variation. The blue lateral body markings (chars. 2, 3 and its inverse, 6) are prounced in the south (Fig. 5A), whilst the blue cheek

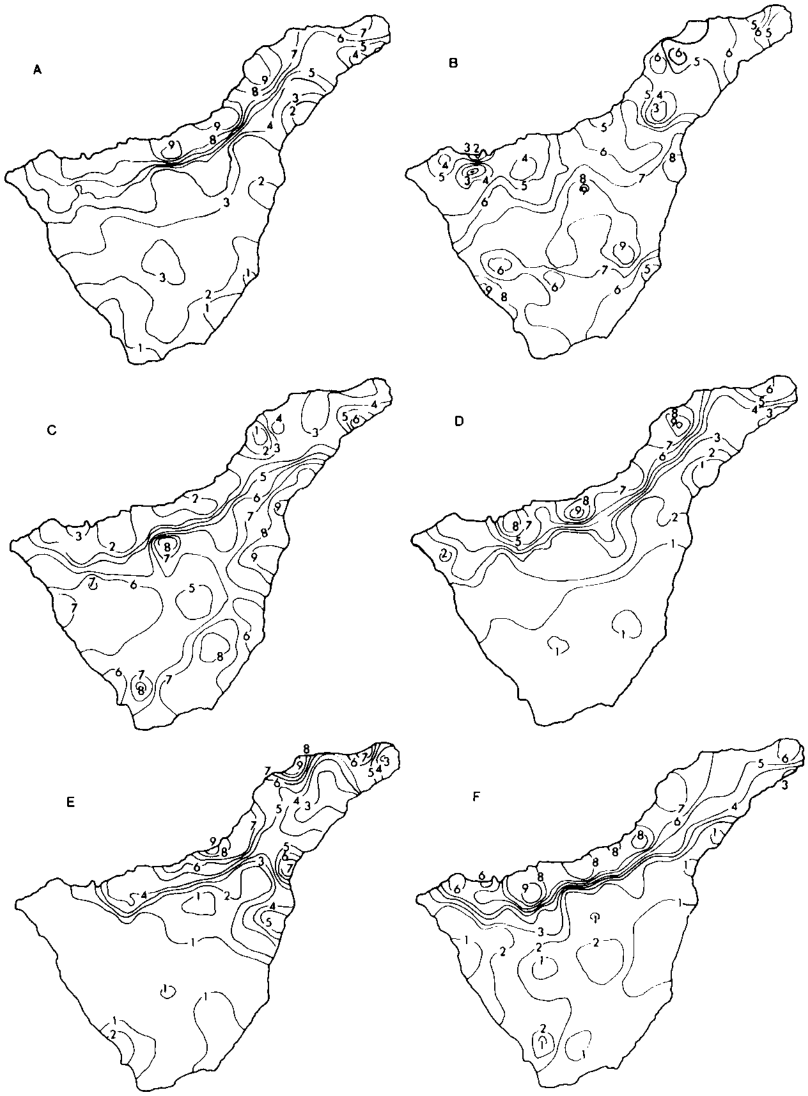

Figure 4. Contours portraying the geographic variation among the 67 locality means of the individual colour pattern characters. The means were scaled on a 0 to 10 range (Table 2). A, Number of yellow bars (char. 1). B, Number of blue blotches (char. 2). C, Size of blue blotches (char. 3). D, Size of yellow bars (char. 4). E, Size of blue chin marking (char. 5). F, Separation of blue blotches (char. 6).

marking (char. 5) and yellow lateral body markings (char. 1, 4) are pronounced in the north (Fig. 5B). The CVA and PCA show that congruence among these patterns is such that the generalized, among-locality, pattern is largely unidimensional, that is, the first canonical variate (CVI) expresses 75% of the among-locality variation. High ordination scores (Fig. 6) indicate well-developed lateral blue markings on the trunk together with poorly-developed blue cheek markings and yellow dorsal bars (Fig. 5A), whilst low scores indicate well-developed blue cheeks and dorsal yellow markings, but poorly developed

TABLE 3. Among-locality correlations of the six colour pattern characters

Char.	1	2	3	4	5
Char. 2	−0.359				
Char. 3	−0.773	0.345			
Char. 4	0.920	−0.354	−0.720		
Char. 5	0.613	−0.160	−0.334	0.639	
Char. 6	0.852	−0.432	−0.827	0.832	0.603

Note. These correlations are based on locality means and indicate the generally high level of congruence in the patterns of geographic variation (d.f. = 65, $P<0.001$ for all except the correlation between characters 2 and 5).

blue markings on the lateral surface of the trunk (Fig. 5B), (eigenvector coefficients for PCI being −0.47, 0.24, 0.42, −0.46, −0.34, −0.47). The contours of the CVI/PCI scores indicate the existance of a 'northern' and 'southern' form with intermediates. The centre of the 'northern' form, that is the form with the lowest CVI/PCI scores is found at middle longitudes on the northern edge of the island. This form changes very sharply to the 'southern' form as one travels directly south up the mountain of Teide but changes more gradually to the intermediate forms as one moves from this point to the east (towards Anaga) and west (towards Teno). In the eastern and western parts of the island the transition between the forms is gradual.

TESTING HYPOTHESES

There are several general problems encountered when trying to test statistically specific hypotheses regarding the cause of patterns of geographic variation by correlating/regressing an observed pattern of geographic variation against a hypothesized pattern.

(1) A complex hypothesis may have to be expressed in a relatively simple quantitative form with an incomplete knowledge of the pertinent evolutionary factors. The pattern has to be hypothesized without using circular logic to make it similar to the observed pattern.

(2) The observed and hypothesized patterns may be coincidentally correlated; that is, if the pattern of geographic variation gives east-west categories due to Pleistocene ice-cap-induced vicariance, then incorrectly hypothesized categories

TABLE 4. Pooled within-locality correlations of the six colour pattern characters

Char.	1	2	3	4	5
Char. 2	0.065				
Char. 3	−0.212	0.208			
Char. 4	0.357	0.020	−0.173		
Char. 5	0.033	0.134	0.185	0.102	
Char. 6	0.133	−0.238	−0.604	0.157	−0.144

Note. These relatively low correlations (except between characters 3 and 6) indicate that the characters express independent facets of the phenotype *sensu* Thorpe (1976).

Figure 5. A, Lateral view of *G. galloti* from the south of Tenerife (El Medano) showing large lateral blue trunk markings. B, dorsal view of *G. galloti* from the north coast of Tenerife (Bajamar) showing lateral yellow bars and some of the blue chin colouration.

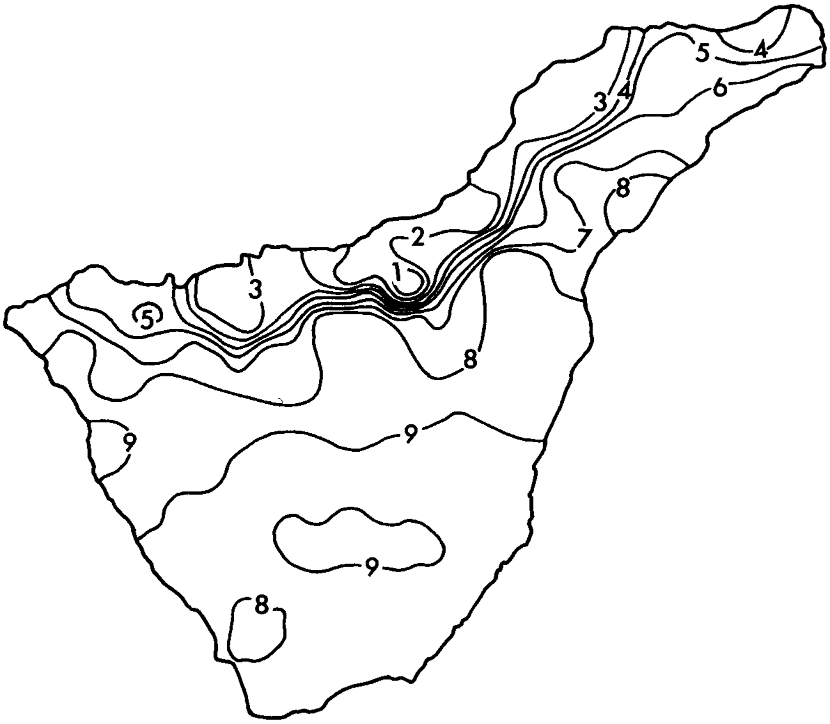

Figure 6. Contours portraying the generalized geographic variation in the colour pattern among the 67 localities (based on locality mean scores of the first canonical variate scaled on a 0 to 10 range).

due to a north-east/south-west river would be significantly correlated given enough sample localities as would an incorrectly hypothesized longitudinal cline. This is related to the problem of multiple hypotheses where patterns derived from several independent hypotheses are significantly correlated to the observed patterns so that one cannot differentiate between them, as found in McKechnie, Ehrlich & White (1975), Douglas & Endler (1982) and Dillon (1984). In some circumstances this problem may be overcome by using multiple regression/partial correlation to test several hypotheses simultaneously. Even so, the value and significance is influenced by what other independent variables are included; the removal of the variable with the highest partial correlation may increase the partial correlation of a previously insignificant independent variable to significance. Consequently, even with partial correlation/multiple regression significance cannot be interpreted as indicating a 'correct' hypothesis. Manly (1986) used this procedure for matrix comparisons, but the number of independent variables (hypotheses) that were tested simultaneously was limited to two.

(3) Some observed patterns and some hypothesized simple patterns, such as a pair of categories, will give 0.1 distribution of values for which parametric statistics such as product-moment correlation, partial correlation and multiple regression are not the most appropriate, particularly when it comes to probability values. Dietz (1983) made some advance with this problem by proposing a series of non-parametric statistics. However, these relate only to

testing one hypothesis at a time; equivalent non-parametric statistics are not available for the important process of considering multiple hypotheses simultaneously (i.e. the equivalent of a non-parametric partial r).

(4) The dimensionality of the hypothesized model and observed pattern can be critical in deciding the appropriate statistical procedure. Some patterns are unidimensional, for example, a simple cline or pair of categories (Thorpe, 1985b, c), whilst others are multidimensional, for example, complex clines (Thorpe, 1987b) or 'isolation by distance' models. Unidimensional patterns are easier to cope with insofar as several hypotheses can be tested simultaneously by multiple regression/partial correlation with unambiguous degrees of freedom. However, when the actual pattern is multidimensional, or multidimensional models are to be tested, then the hypotheses can be tested by comparing the distance matrices which represent the degree of observed and hypothesized dissimilarity between sample localities. When this is done, the degrees of freedom are not apparent because of the non-independence of the units within a matrix. This problem can be tackled by Mantel's test and related statistics (Sokal, 1979; Douglas & Endler, 1982; Dietz, 1983; Dillon, 1984; Manly 1986) for both parametric and non-parametric situations. The emphasis on solving the problems of comparing distance matrices has obscured the fact that this may be neither necessary, nor desirable, in some circumstances. Even when the observed pattern is defined by multivariate methods the pattern may be unidimensional, that is, adequately expressed by one vector such as a principal component or canonical variate. Moreover, even if the pattern is multidimensional, each component/variate may express a different facet of the pattern which is, in turn, the product of a different cause. In these circumstances, the complications and limitations of comparing matrices may be best avoided (e.g. packages are not available for testing more than two matrix-defined independent hypothesis simultaneously).

Hypotheses—methods

In this case, the observed pattern of geographic variation is largely unidimensional as are all the pertinent hypothesized patterns. Consequently, the series of hypotheses were tested simultaneously by computing their partial correlation with the observed pattern of each individual character. The hypotheses were also tested against the observed generalized geographic variation in the colour pattern as defined by the first canonical variate. The second canonical variate also portrays some residual among-locality variation so the hypotheses were also tested against this. There are seven hypotheses and testing these against eight characters/variates gives 56 partial correlations. With $P < 0.05$ for rejecting the null hypothesis one would expect approximately three significant correlations by chance, so $P < 0.01$ is taken as the level at which a null hypothesis of no correlation is rejected. The partial correlation is computed across the 67 (type B + C, Fig. 1) localities. The hypotheses are as follows.

Hypotheses 1, 2 and 3. The ancient precursor islands of Anaga (east) and Teno (west) were joined to form the island of Tenerife when the volcanic mountain Teide erupted between them *c.* two million years ago (Borley, 1974). Following Machado's (1976) discussion of this event in relation to the biogeographical patterns of ground beetles in Tenerife, Bischoff (1982) suggested

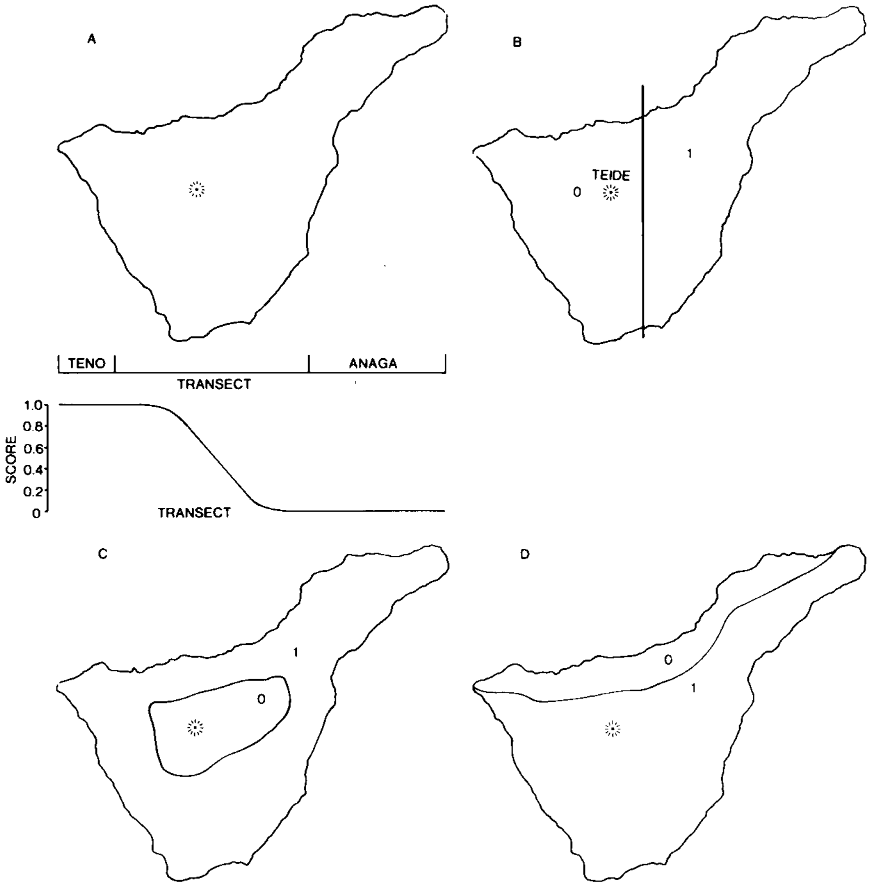

Figure 7. A representation of some of the hypothesized patterns of geographic variation. A, Hypothesis 2, showing that a longitudinal transect gives an S shape transition between precursor populations in the east and west. B, Hypothesis 3, gives two parapatric categories that meet mid-point between Anaga and Teno. C, Hypothesis 4, gives a high altitude and low altitude categories based on the altitudes in Pasteur and Salvidio (1985). D, Hypothesis 6, gives the categories based on topographically determined climate.

that the cause of the geographic variation in the colour pattern of *G. galloti* could be secondary contact between the already differentiated stocks of Anaga and Teno. Since Anaga lies in the extreme east and Teno in the extreme west this hypothesizes a longitudinal pattern of differentiation. The exact nature of the hypothesized pattern depends on the extent of introgression. Strong gene flow without genetic barriers to interbreeding would result in a gradual longitudinal cline. Hypothesis 1 is therefore a cline with the scores for the localities being their longitudinal position (low west, high east). Limited introgression would result in a more S-shaped transition across a contact zone (Thorpe, 1979, 1987c) as in hypothesis 2 (Fig. 7A), with the Teno scores as one, changing according to the S curve, to zero in Anaga. A complete absence of introgression would lead to two parapatric categories, one eastern (scored as one), the other western (scored as zero). Hypothesis 3 is therefore an eastern category and a western category which meet at the mid-longitudinal point between the inner edges of Anaga and

Teno (Fig. 7B). These hypotheses are all simple and an intermediate condition between them could exist. Nevertheless, if this phylogenetic/historical scenario is correct then these three hypotheses would bear sufficient resemblance to the actual pattern to give positive results.

Hypothesis 4. Pasteur & Salvidio (1985) suggest that the mid-altitude ground-level cloud layer results in two allopatric populations, a low-altitude population below the cloud layer and a high-altitude population above the cloud layer. Hypothesis 4 is therefore a low-altitude category (scored as one) and a high-altitude category above the ground-level cloud (scored as zero), based on the altitudes in Pasteur & Salvidio (1985) as illustrated in Fig. C.

Hypothesis 5. There are differences in climate within Tenerife related to altitude, particularly humidity and the extent of diurnal and seasonal rhythms (Huetz de Lemps, 1969). Other features of this lizard, i.e. some scalation characters (Thorpe & Baez, 1987), are adapted to altitude. The scores for hypothesis 5 are taken as the altitude in an attempt to test whether it also contributes to the determination of the colour pattern.

Hypothesis 6. This hypothesis is based on adaptation to the biotic effects of the topographically determined climate. The most dominant climatic feature of Tenerife is the remarkable difference between the north-facing slopes below 1500 m, which have a semi-permanent cloud cover, and the rest of the island (Huetz de Lemps, 1969). The predominant winds produce a latitudinal climatic difference within most of the Canary Islands, but the considerable height of Tenerife and consequent inversion zone at 1500 m makes the extent of the difference greater and the transition sharper.

Owing to this cloud cover, the north-facing slopes below 1500 m (NFS) are cool/warm, with relatively high humidity and low insolation. On the NFS the vegetation is lush; the 1500 m contour broadly defines the limit of the luxuriant natural 'laurel forest' (Kammer, 1974). On the rest of the island, that is, the north-facing slopes above *c.* 1500 m and the south-facing slopes, the island is generally hot, arid and rather barren. Hypothesis 6 therefore predicts a simple categorical pattern consistent with this topographically-determined climate variation, with the NFS below 1500 m scored as zero and the rest of the island as one (Fig. 7D).

The following scenario links the pattern of variation for hypothesis 6 with the direction of character-state change, by suggesting that the topographically determined climate influences the balance between sexual selection for intra-specific signalling colouration and natural selection for cryptic (anti-predator) colouration. Females and sexually immature males have cryptic colouration and behaviour to minimize predation, largely from aerial predators such as kestrals (*Falco tinnunculus*) which predate *G. galloti* (Bacallado & Dominguez, 1984). In contrast, sexually mature males in breeding colour select prominent positions on the tops of rocks and walls to bask and display for sexual/territorial purposes (Molina Borja, 1985) and this may expose them to a greater risk of predation, particularly post-emergence before they have reached their activity temperature range. The importance of thermoregulation to predation avoidance in lizards is documented in Losos (1988) and references therein. On these cloudy north-facing slopes, difficulty in gaining heat (e.g. in the critical post-emergence period) may make it more difficult to avoid predation and put a greater premium on cryptic colouration. Also, the luxuriant vegetation of the north-facing slopes may render a disruptive colour pattern more effectively cryptic than in the barren south. Whatever the precise selective mechanism aerial predators see predominantly the dorsal surface of the lizard whilst the conspecific sexual/territorial competitors and potential mates see predominantly the lateral surface of the lizard.

In this 'sexual selection versus predation' scenario the yellow cross markings of sexually mature males, being predominantly dorsal, serve the purpose of disruption/crypsis. Consequently, they are most pronounced on the cloudy, well-vegetated, north-facing slopes, to avoid the increased risk of aerial predation in critical periods, and/or because the disruptive yellow marks are more effectively cryptic against the luxuriant vegetation. The blue markings on the trunk (chars. 2, 3, 6), being predominantly lateral, are for intra-specific communication, that is sexual/territorial display. They are undeveloped on the north-facing slopes because they would be obscured by the yellow trunk markings, but developed in the rest of the island. Finally, the lizards on the north-facing slopes have developed blue cheek markings (char. 5) for sexual/territorial purposes to compensate for the lack of blue trunk markings, whilst in the rest of the island (where blue trunk markings are found) no blue cheek markings are necessary. Note that, like the previous hypotheses, the pattern is hypothesized *a priori*, but in this case a scenario explains the direction of change in individual characters as well as the pattern of geographic variation.

Hypothesis 6 is over-simplified as it assumes a sharp change between ecotones and does not allow for any gene flow. The former is fairly realistic in the regions where there is a sharp change between cloudy and non-cloudy areas, but the both gene flow and a more gradual change in ecotones are possible in the regions of high population density outside the middle altitude ground-level cloud layer of Teide. Consequently, as with the Anaga/Teno models, an additional model that hypothesizes complete introgression is included. This model hypothesizes (hypothesis 7) a smooth cline with the scores determined by the latitude.

Hypotheses—results and conclusions

All three hypotheses (1, 2, 3) based on the 'phylogenetic' or historical model of secondary contact between populations from Anaga and Teno (Bischoff, 1982), with varying degrees of introgression, show no significant partial correlation with any of the six characters or two canonical variates (Table 5). One can therefore conclude that this is not the cause of any of the geographic variation in individual colour pattern characters or the cause of the generalized pattern of geographic variation (as expressed by CVI) or residual variation (as expressed by CVII). Similarly, the hypothesized (4) allopatry between low- and high-altitude populations due to the ring of mid-altitude ground-level cloud (Salvidio & Pasteur, 1985), is not significantly partially correlated to any of the six individual characters of two canonical variates (Table 5) and is rejected as the cause of any of the geographic variation in the colour pattern. The same is true of hypothesis 5 as there is no significant parital correlation at $P<0.01$ between altitude and any of the characters of canonical variates (Table 5).

However, for the generalized pattern of geographic variation (CVI) and all individual characters (except char. 2) the topography/climate hypothesis (6) gives the highest (CVI, chars. 1, 4), or only significant, $P<0.01$, (chars. 3, 5, 6),

TABLE 5. Partial corelations between the seven hypotheses and eight characters/canonical variates

	Characters						Canonical variates	
	Ch 1	Ch 2	Ch 3	Ch 4	Ch 5	Ch 6	CVI	CVII
Hypotheses								
1	−0.152	0.101	−0.081	−0.020	0.214	0.199	−0.110	0.211
2	−0.216	0.041	−0.136	−0.248	−0.099	−0.002	0.160	−0.067
3	−0.155	0.101	0.014	−0.223	−0.062	−0.205	−0.206	−0.012
4	−0.156	−0.080	−0.129	−0.265	−0.113	0.032	0.139	−0.064
5	−0.039	0.034	−0.171	−0.176	−0.275	0.012	0.154	−0.265
6	*−0.671	0.021	*0.616	*−0.711	*−0.341	*−0.634	*0.689	0.227
7	*0.500	*−0.319	−0.236	*0.384	0.200	0.203	*0.382	−0.031
MULT R	0.860	0.335	0.764	0.860	0.614	0.761	0.862	

Note. An asterisk indicates significant partial correlations at $P<0.01$. The multiple correlation (MULT R) between only the significant hypotheses (at $P<0.01$) and each characters/variates is given. The hypotheses, characters (Ch) and canonical variates (CV) are explained in the text.

partial correlation (Table 5). Therefore, one cannot reject this as the primary cause of these patterns of geographic variation. Moreover, the direction of change is also consistent with the sexual selection/predation scenario linked with hypothesis 6. Both the number (char. 1) and size (char. 4) of the yellow markings are more pronounced in the high cloud ‘north’ giving high negative partial correlations with the pattern of hypothesis 6, which is consistent with the sexual selection/predation scenario (Table 5). Also, both the size (char. 3) and degree of separation (char. 6) of the blue trunk markings, vary in a direction consistent with the sexual selection/predation scenario, and give significant positive and negative partial correlations respectively with the pattern of hypothesis 6. Similarly, the blue cheek marking (char. 5) is well developed in the north consistent with the sexual selection/predation scenario and has a significant partial correlation with the pattern of hypothesis 6.

Hypothesis 7 is also significantly partially correlated (Table 5) with the patterns of variation of the yellow dorsal markings (char. 1, 4) and the generalized pattern of geographic variation (CVI), albeit at a much lower level than hypothesis 6. This may be because of smoothing effect of gene flow, and/or a more gradual transition between ecotones than is allowed for in hypothesis 6, introducing an element of a latitudinal cline into the pattern.

Character 2, the number of blue trunk markings, is the only character not, at least partly, explained by the simple categorical pattern of the topography/climate model of hypothesis 6. Although, this character is partially correlated to the clinal associate of this model, i.e. hypothesis 7 (Table 5). Even so, this partial correlation is low and the geographic variation in this character may be caused, at least in part, by factors not considered in this study.

The residual among-locality variation expressed by the second canonical variate is not significantly partially correlated to any of the hypotheses at $P<0.001$, although its highest partial correlation is with altitude.

GENERAL DISCUSSION

It is clear that there is considerable microgeographic variation in the colour pattern of sexually mature males of *Gallotia galloti* within the island of Tenerife, that there is generally high congruence among the patterns of geographic variation in individual colour pattern characters and that the generalized geographic variation in the colour pattern is basically unidimensional and expressed by the first canonical variate of principal component. The existence of microgeographic variation in the colour pattern conforms to the findings of a previous study of this island population (Thorpe & Baez, 1987) which found microgeographic variation in the scalation, size and shape. It does, however, run counter to the implicit assumption of within-island homogeneity that underpins so many studies of evolution in island archipelagoes.

Other than the above study of scalation, size and shape, previous hypothesized causes of geographic variation of this species within Tenerife have been based on the assumption of the importance of gene flow; a view that was predominant prior to Ehrlich & Raven (1969). Both the Anaga/Teno hypotheses (Bischoff, 1982) and the high-altitude/low-altitude hypothesis (Pasteur & Salvidio, 1985) are based on differentiation in allopatry, albeit with different patterns and mechanisms. All three variations of the Anaga/Teno hypotheses are rejected as the cause of the generalized pattern of geographic variation (CVI) as well as being rejected as the cause of the geographic variation in all of the individual characters. The relatively slight geographic variation does not require the extensive time involved (*c.* two million years) to develop, as geographic variation can develop rapidly and even incipient speciation can take much less time (Thorpe & Baez, 1987 and references therein). Similarly, the low- and high-altitude populations are shown not to be allopatric and this hypothesized cause is rejected statistically for the generalized pattern of geographic variation as well as for all of the individual characters (even so, where the ground-level cloud and 'transition zone' coincide on the northern slopes of Teide (Fig. 3), the drop in population density may have resulted in the sharper transition found in this region). Therefore, all of the 'allopatry' hypotheses are clearly untenable.

The topography/climate hypothesis cannot be rejected as a cause of the geographic variation in the colour pattern. This hypothesis does not assume differentiation in allopatry but this does not mean that the level of gene flow, restricted in regions of very low population density, has not influenced the pattern of geographic variation. One can see from Fig. 3 that, although the mid-altitude ring of low population density cannot explain the pattern of geographic variation, its northern face partially coincides with the transition zone between colour forms. Whilst this is predicted by the topography/climate hypothesis, it should be borne in mind that such regions of low population density can sustain or reinforce transition zones (Womble, 1951) and that modelling suggests that it may even attract them if they are close enough (Brues, 1972).

The simple formulation of the topography/climate hypothesis is rather unrealistic in giving a sharp categorical pattern and not allowing for gradients in the selection, or the effects of gene flow. If one assumes that gene flow can smooth the transition between forms and that it is reduced in regions of lower population density then one can make some predictions regarding the pattern of geographic variation. One would predict that the transition zone would be sharpest where it coincides with the trough of low population density on the north face of Teide and this is what occurs. One would also predict that gene flow would result in more intermediate values in Anaga and Teno than on the narrow low-altitude strip to the north of Teide and this also occurs. Both of these predicted facets can be seen in the generalized pattern of geographic variation

(CVI) and in the individual characters to a varying extent. Consequently, the statistical analyses not only support primarily the topographic/climate hypothesis, but secondarily the more gradual transition of hypothesis 7, for the generalized pattern and some of the individual characters. This simple formulation of the topography/climate hypothesis has therefore led, in some characters and the generalized pattern, to the acceptance of two hypotheses rather than one, even though partial correlation was employed. One solution to this may appear to be to permutate generation number, selection coefficient and gene flow extent in a computer simulation until the hypothesized pattern closely resembles the observed pattern. However, this would involve the problem of circular logic mentioned in the section on 'Testing Hypotheses', above.

The influence of topographically determined climatic conditions on the balance between sexual selection and predation has not previously been suggested as the cause of any geographic variation of the colour pattern or any other characteristic of this island population. Nevertheless, the balance between selection for attractiveness and natural selection to avoid predation by crypsis, has been hypothesized as the cause of geographic variation in other situations, for example, Endler's (1978, 1980, 1983) work on guppies.

Although the individual colour pattern characters generally have congruent patterns of geographic variation, the number of blue trunk markings (char. 2) has the lowest congruence with other characters and is the exception in not being explained by the topography/climate hypothesis. As one would expect from geographic variation caused by natural selection rather than phylogenesis (Thorpe, 1987a), other characteristics do not necessarily show congruent patterns. The clear altitudinal element of the geographic variation in the scalation (Thorpe & Baez, 1987) is not apparent in the colour pattern of sexually mature males even though CVII and character 5 are just sub-significantly correlated with altitude in this study ($0.01<P<0.05$). Similarly, the colour pattern does not show any pattern of geographic variation that is similar to the cline in body proportions in this island population (Thorpe & Baez, 1987). Nevertheless, there is a latitudinal element in the pattern of geographic variation in the scalation (Thorpe & Baez, 1987) that resembles the latitudinal pattern of geographic variation in the colour pattern. Given that climate is implicated as a cause of geographic variation in the number of scales in lizards via desiccation effects (Thorpe & Baez, 1987 and references therein), topographically determined climate may be a causative factor common to both colour and scalation variation.

The topography/climate hypothesis and sexual selection versus crypsis scenario are clearly involve a 'current ecological ' cause rather than a 'phylogenetic' cause. Other, eclectic, evidence also points to the cause being current ecology rather than historical/phylogenetic. Several of the Canary Islands have reptile populations showing latitudinal variation related to climate. Since these islands have an independent geological history this parallel variation cannot be due to a historical event common to all islands. Also, the degree of incongruence among character systems in unlikely for phylogenetically caused variation (Thorpe, 1984, 1987; Thorpe & Baez, 1987); the time factor involved in phylogenetic hypotheses 1–3 is extremely large when considering the rather subtle variation and phylogenetic hypothesis 4 is not supported by observations on the distribution of the demes.

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