Testing hypothesized causes of within-island geographic variation in the colour of lizards

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Received 20 September 1988; accepted 20 December 1988

Summary. Within the island of Tenerife the lizard *Gallotia galloti* shows geographic variation in a range of features, most notably the colour pattern of breeding males. Numerous (7) specific causal hypotheses, both phylogenetic and ecogenetic, are proposed or plausible for this geographic variation and these are simultaneously tested against the observed multivariate pattern. The hypotheses based on the divergence in allopatry (e.g. the secondary contact of populations from the precursor islands of Anaga and Teno and the separation of high- and low-altitude populations by encircling cloud) are rejected. The hypothesis that the pattern is caused by topographically determined climatic differences within the island is not rejected. The climate may influence the balance between selection for signalling colouration for sexual/territorial purposes and natural selection for crypsis.

Key words. Geographic variation; natural selection; sexual selection; multivariate analysis; crypsis.

The study of geographic variation within individual islands has practical advantages. Since the number of species tends to be low the abundance of individuals per species tends to be high; this is an advantage when obtaining samples for quantitative work. Moreover, environmental conditions and character states can change over very short distances with consequent logistic advantages.

On the island of Tenerife (Canaries) the lizard *Gallotia galloti* is very abundant and shows spatial heterogeneity (microgeographic variation) in a range of features[1–3], the most obvious of which is the colour pattern of sexually mature males[4]. Whilst the colour pattern and behaviour of juveniles and females is cryptic to avoid predation from mainly aerial predators, e.g. *Falco tinnunculus*, breeding males adopt prominent positions and are boldly coloured. In these males the background colour is very dark and, depending on locality, the trunk can be overlaid with lateral blue blotches or alternatively mainly dorsal yellow cross bars (plus a blue lateral surface to the cheek).

Pattern of microgeographic variation. Six unit characters represent the colour pattern of mature males: 1) number of yellow bars, 2) size of the yellow bars (in dorsal scales), 3) the number of blue lateral blotches, 4) size of the blue lateral blotches (in dorsal scales), 5) separation (inverse of size) of the blue lateral blotches, and 6) size of the lateral blue chin marking (in scales). These characters were recorded from high quality macrophotographs of over 500 live mature male lizards from 67 representative localities throughout Tenerife. Pooled within-locality correlations are very low showing these characters to be independent elements of information[5, 6] (except 4 and 5) and among-locality correlations are high (except 3) showing that they have generally congruent patterns of geographic variation[5-7].

The generalized pattern of geographic variation across the six-colour pattern characters is analyzed by canonical variate analysis treating each of the 67 locality samples as a group. This ordination technique takes into account the within-group covariance among characters and summarizes the variation among the predefined groups in orthogonal axes expressing progressively less variation[8]. The generalized geographic variation in the colour pattern is largely unidimensional and consequently is adequately defined by the first canonical variate (fig.). These results are confirmed by principal component/coordinate analysis of standardized locality means[8] (r between PCI and CVI = 1.0) which gives normalized eigenvector coefficients for the six characters (– 0.47, – 0.46, 0.24, 0.42, – 0.47, –0.34). The score for a locality mean along this canonical variate defines the general or overall state of the colour pattern at that locality – a low score indicates well-developed yellow dorsal cross bars and blue lateral cheeks and minimal blue lateral trunk markings whilst a high score indicates the opposite (fig.).

Hypothesis testing. A range of hypotheses have been, or could be, erected to explain the cause of microgeographic variation within this island population. Hypothesis testing can be difficult in evolutionary work but in geographic variation analysis causal hypotheses can sometimes be tested by correlating or regressing the observed pattern with the pattern generated from a hypothesized cause.

One of the problems with this procedure is that several 'erroneous' alternative hypotheses can be accepted along with the 'correct' hypothesis because they predict patterns that are coincidentally not independent of the observed pattern, i.e., several predicted patterns are correlated.

When there are multiple hypotheses this can lead to several alternative hypotheses being accepted[9-11]. This problem can be minimized by using multiple regression/partial correlation to simultaneously consider several hypotheses. When the patterns are represented by similarity/distance matrices the non-independence of the values necessitates the use of a Mantel-style statistic[9, 11-14] but to date only two independent matrices have been tested simultaneously[14]. In this case there are seven hypotheses and since they and the observed pattern are unidimensional the hypotheses (independent) can be simultaneously tested by partial correlation with the observed (dependent) pattern.

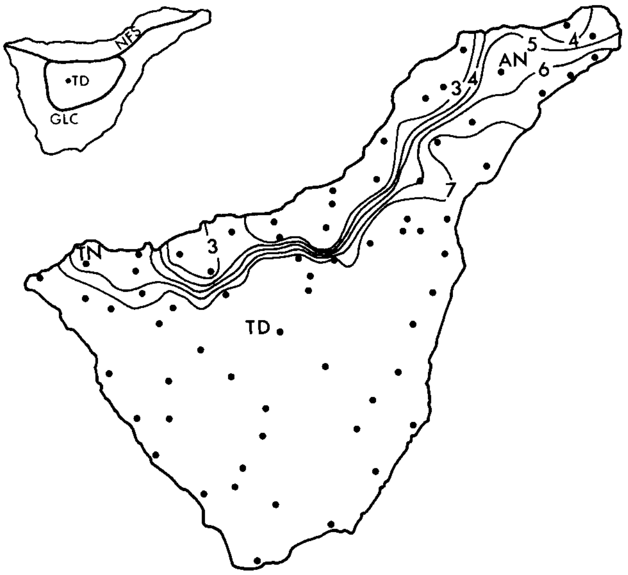
The observed pattern (the dependent variable in the partial correlation, table) of variation among the 67 localities is represented by the locality mean scores of the first canonical variate, i.e., the group centroids. Seven hypothesized patterns (the seven independent variables in the partial correlation, table) of variation among the 67 localities are derived in turn from the following seven hypotheses:

Hypotheses 1, 2 and 3. A suggested[4] cause of the geographic variation in the colour pattern is that the islands of Anaga (east) and Teno (west) had differentiated allopatric populations of *G. galloti* that met secondarily after these two precursors were joined to form Tenerife by the eruption of Teide circa two million years ago[15]. Complete introgression after this secondary contact predicts a gradual longitudinal cline (hyp. 1) between the eastern and western precursors. The independent variable representing hypothesis 1 in the partial correlation (table) is therefore the longitudinal position of each of the 67 localities. Limited introgression (hypothesis 2) predicts an S shape transition[16-18] between the precursors. The independent variable representing hypothesis 2 in the partial correlation (table) therefore describes a sigmoid curve, with the localities in the west (Teno) scored as unity and the localities in the east (Anaga) scored as zero. The inflexion of the curve (scored as 0.5) is positioned mid-longitude between the inner edges of Teno and Anaga. A complete lack of introgression (hypothesis 3) between the precursors predicts east-west parapatric categories. The independent variable representing hypothesis 3 in the partial correlation (table) therefore has eastern localities scored as unity and western localities scored as zero; with the abrupt change occurring mid-longitude between the inner edges of Teno and Anaga.

Partial correlations between the hypothesized patterns and the generalized pattern of geographic variation

Hypotheses	1	2	3	4	5	6	7
Partial r	−0.110	0.160	−0.206	0.139	0.154	*0.689	*0.382

In the partial correlation analysis the locality scores for the generalized pattern are group centroids for the major canonical variate (fig.) and the locality scores for the variables representing the hypotheses are: 1) longitude; 2) Teno scored as one changing through a sigmoid curve (with the inflexion mid-point between the inner edges of Anaga and Teno) to zero in Anaga; 3) east scored as one changing abruptly at the mid-point between the inner edges of Anaga and Teno to zero in the west: 4) low altitude (below 1500 m) scored as one, high altitude as zero (fig.); 5) altitude; 6) north facing slopes below 1500 m scored as zero and elsewhere as one; 7) latitude. An asterisk denotes significance at $p < 0.01$.



Generalized pattern of geographic variation. The canonical variate scores are coded on a 0–10 scale and the transition zone is portrayed by isophene contours 3 to 7. The positions of Anaga (AN), Teno (TN), Teide (TD) are given, as are the localities (dots) at which the colour pattern was studied. The inset indicates the division (NFS) between north facing slopes below 1500 m and elsewhere and also gives the approximate position of ground-level cloud (GLC) hypothesized to separate high and low altitude populations. To the north of the transition the males in breeding colour have predominantly dorsal yellow cross bars on the trunk and blue lateral cheeks whilst to the south of the transition these elements are minimal and the trunk has large lateral blue blotches.

Hypothesis 4. Researchers studying isozyme differentiation[3] have suggested that lizards are absent from an area covered by a ring of mid-altitude ground-level cloud around Tenerife and that the purported allopatry between the high- and low-altitude populations is the cause of the differentiation. This hypothesis predicts distinct altitudinal categories (one high- and one low-altitude). The independent variable representing hypothesis 4 in the partial correlation (table) therefore has localities above the ground level cloud (fig., inset) scored as zero and those below scored as unity.

Hypothesis 5. It is hypothesized that altitudinal differences in the climate[19] could cause a gradual altitudinal cline (as is found in the scalation[2]). The independent variable representing hypothesis 5 in the partial correlation (table) is therefore the altitude of each of the localities in metres above sea level.

Hypothesis 6. This predicts differences between samples from the north facing slopes (NFS) below 1500 m (fig., inset) and the remaining range because there are dramatic climatic differences, i.e., the NFS generally have high cloud cover below 1500 m and are therefore cooler, humid and well vegetated (the locality of the original laurel forest[20]) whilst elsewhere (including the high-altitude NFS) it is generally sunny, hot, arid and barren. The pattern hypothesized by adaptation to these topographically determined climatic conditions is a pair of latitudinal categories which are separated by the 1500-m contour on the NFS (fig., inset). The independent variable representing hypothesis 5 in the partial correlation (table) therefore has scores of zero for the localities in the northern category and scores of unity for localities in the southern category. The climate may influence the balance between selection for signalling coloration for sexual/territorial purposes and natural selection for anti-predator crypsis. On the cloudy NFS the lizards, being heliotherms, have difficulty in gaining sufficient heat in the critical post-emergence period to avoid predation thereby putting a greater premium on crypsis in these areas. Also disruptive colouration may be more effective against the well-vegetated background of the NFS than the barren background[21] found elsewhere. Whatever the relative importance of these mechanisms, conspecifers will view one another laterally whilst the predators (kestrels) will view predominantly the dorsal surface of a lizard. This suggests the geographic pattern and direction of individual character change as follows. The predominantly dorsal yellow cross bars will have maximum development for disruptive cryptic colouration on the NFS to minimize predation and minimum development elsewhere. The lateral blue markings on the trunk will have minimum development in the north because they would be compromised by the yellow markings, but will have maximum development elsewhere for sexual attractiveness/territorial display. To compensate for the minimized blue trunk markings on the NFS specimens the blue cheek marking will be maximized for sexual attraction/territorial display. Given the character weighting in the ordination analysis (above) this predicts high ordination scores in the southern category and low scores in the northern category, i.e., a positive partial correlation with the observed pattern.

Hypothesis 7. The above hypothesis (6) not only assumes a sharp change between ecotones but does not allow for gene flow effects. This hypothesis therefore assumes complete introgression between the latitudinal forms resulting in a smooth cline. The independent variable representing hypothesis 7 in the partial correlation (table) is therefore the latitude of each of the localities. Given the character weighting in the ordination analysis (above) a positive partial correlation is expected.

The hypotheses (1, 2 and 3) based on the phylogenetic model of secondary contact between Anaga and Teno populations are rejected by partial correlation analysis as is the other hypothesis (4) that proposes differentiation in allopatry, i.e., altitudinal categories due to separation by ground-level cloud (table). The hypothesis that the geographic variation is caused by adaptation to altitude (hyp. 6) is also rejected (table). The hypothesis that the variation in the individual characters and generalized pattern (table) is due to topographically determined climatic differences cannot be rejected. It appears that the climate influences the balance between sexual selection for signalling colouration and natural selection for disruptive cryptic colouration to minimize predation. This hypothesis (6) has the highest and most significant partial correlation with the generalized pattern and all individual characters, except for the number of blue blotches. Lower, but significant, partial correlations are found between hypothesis 7 and the size and number of yellow cross bars and also the generalized pattern, so one cannot reject the hypothesis of substantial introgression (or a more gradual transition in the ecotones) in these cases. The rejected allopatry hypotheses (1–4) are also unlikely on other grounds. The time factor for hypotheses 1–3 is gross in relation to the relatively subtle variation[2]; the populations are in fact not separated into allopatric altitudinal categories (hyp. 4); the degree of incongruence between character systems is unlikely for allopatric (phylogenetic) causation[1, 2, 5]; and the latitudinal variation in the herpetofauna of adjacent islands cannot be due to a common historical event as each island has its own geological history.

This study of geographic variation within an island provides an example of how complex phenotypic features may be a compromise between specific selective forces, and raises, for the first time, the possibility of climatic factors influencing the balance between sexual selection and crypsis. The balance between sexual selection and natural selection is also thought to cause geographic variation in the colour pattern of guppies[9, 22–24]. In the guppy case multiple alternative hypotheses have been tested, but not simultaneously[9]. It can be particularly difficult to distinguish between causative factors in geographic variation analysis[1, 5] but the relatively simple procedure used in this study proved to be very effective for simultaneously testing multiple hypotheses when the patterns are unidimensional.

Acknowledgment. We wish to thank the Royal Society, the Consejo Superior Investigaciones Cientificas and the Carnegie Trust for grant support (to R.S.T.), and Marcos Baez for his assistance.

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0014-4754/89/040397-04$1.50 + 0.20/0