

Within-island microgeographic variation in the colour pattern of the skink, *Chalcides sexlineatus*: Pattern and cause

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Abstract

The colour pattern of the Gran Canarian skink is described with eight independent colour pattern characters. Significant geographic variation occurs in each character. There are generally high levels of congruence between the patterns of geographic variation in each character although some differences exist. In canonical variate analyses, the first canonical variate expresses most of the among-locality variation in colour pattern, indicating a largely unidimensional pattern. Patterns of geographic variation in the colour pattern are portrayed by contouring. This reveals north-east/south-west clines for seven of the individual characters and the generalized pattern (CV1). Four causal hypotheses were erected which predicted four different unidimensional patterns of geographic variation. Mantel tests and partial correlation analyses were used to compare the observed patterns of microgeographic variation with the four hypothesized patterns. This method suggests differential selection occurring between ecotones as the cause of the microgeographic variation. Microgeographic variation in some aspects of the colour pattern can be explained by selection for different anti-predator strategies in the hot, arid southern areas vs the cooler, lush northern areas.

Introduction

Many evolutionary studies have concentrated on among-island microgeographic variation to test theories about dispersal and microevolution (e.g. Grant et al.,

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1985; Clover, 1979; Ricklefs and Cox, 1972). However, until recently, vertebrate within-island geographic variation has received very little scientific attention. For the evolutionary biologist, geographic variation occurring within small islands has several advantages over that occurring over larger geographical distances. These are: 1) higher population densities of island species mean that locality samples are more readily obtained; 2) substantial geographic variation can occur over very short distances giving logistic advantages; and 3) the limited nature of the geographic variation enables a detailed description of the pattern, which is useful when attempting to determine the cause.

Causes of described geographic variation are often inferred by visual analyses of the patterns. For example, selection for current ecological conditions is often forwarded as an explanation where a species shows increasing body size with latitude (e.g. Wooller et al, 1985). However, a more rigorous approach is to numerically test the described patterns against different models (Douglas and Endler, 1982). Mantel Tests (Mantel, 1967; Manly, 1986) are most suitable for this as they compute measures of association between different matrices, which are then compared with the same measures computed after randomization of the matrices. For unidimensional matrices, partial correlation analysis has also been shown to be extremely useful for causal hypothesis testing in some situations (Thorpe and Brown, 1989a, b).

Current studies on the Canary Island herpetofauna indicate that large differences in selection pressures occur within the small heterogenous islands, which give rise to the considerable within-island microgeographic variation seen in several species there (Thorpe and Báez, 1987; Thorpe and Brown, 1989a, 1989b; Brown and Thorpe, 1990; Thorpe, 1991). Confirmation that observed microgeographic variation is caused by differential selection comes from the close relationships found between patterns of morphological variation and patterns of current ecotypic variation on the islands. On the Canary Island of Tenerife, the substantial differences in climate and vegetation between the low/middle altitude northern slopes and the rest of the island is the primary cause of the microevolution in colour pattern of the lizard *Gallotia galloti* (Thorpe and Brown, 1989a, 1989b). On the adjacent island of Gran Canaria, the microgeographic variation in body proportions and scalation of the endemic skink, *Chalcides sexlineatus*, covaries with the north/south variation in climate and vegetation (Brown and Thorpe, 1990). In addition, the number of body scales in this species increases with altitude.

Considerable microgeographic variation in the colour pattern of *C. sexlineatus* has been commented on by several authors (e.g. Steindachner, 1891a, b; Lopez-Jurado and Báez, 1985) although a quantitative description has never been made. Lopez-Jurado and Báez (1985), in a qualitative study, attempted to summarize the microgeographic variation in *C. sexlineatus* by grouping sample localities into six geographical areas according to observed colour pattern differences. Pasteur, Keymar and Perret (1988) used some colour pattern characteristics as evidence to support a proposal that more than one species of *Chalcides* exists on Gran Canaria. Their hypothesis has since been shown to be unlikely in light of the geographic variation in body proportions and scalation (Brown and Thorpe, 1990).

This study quantifies the main features of the colour pattern so that the geographic variation in this character system can be numerically described. Several plausible causal hypotheses will be simultaneously tested against the observed pattern(s) of microgeographic variation, using partial correlation and Mantel tests. Comparisons will then be made with microgeographic variation in body proportions and scalation of *C. sexlineatus*, and in the colour pattern of *Gallotia galloti*, the lacertid on the adjacent island of Tenerife.

Materials and methods

Specimens and characters

The colour patterns of 691 *C. sexlineatus* were recorded against a constant background using macrophotography. The animals were from 47 evenly distributed localities which covered most parts of the island (Fig. 1). The colour pattern photographs were analyzed and the following eight characters recorded:- (C1) Extent of blue pigment on the ventral surface. Ventral blue pigment spreads up the belly from the cloaca to the chin. This was scored from zero (absence of ventral blue pigment) to five (ventral blue pigment extending up to chin); (C2) dorsal tail colour. Tail colour varies from brown, through green (intermediate hue), to deep-blue. Scores ranged from zero (brown tail) to four (deep-blue tail); (C3) extent of ventral orange pigment. Orange pigment spreads down the belly from the

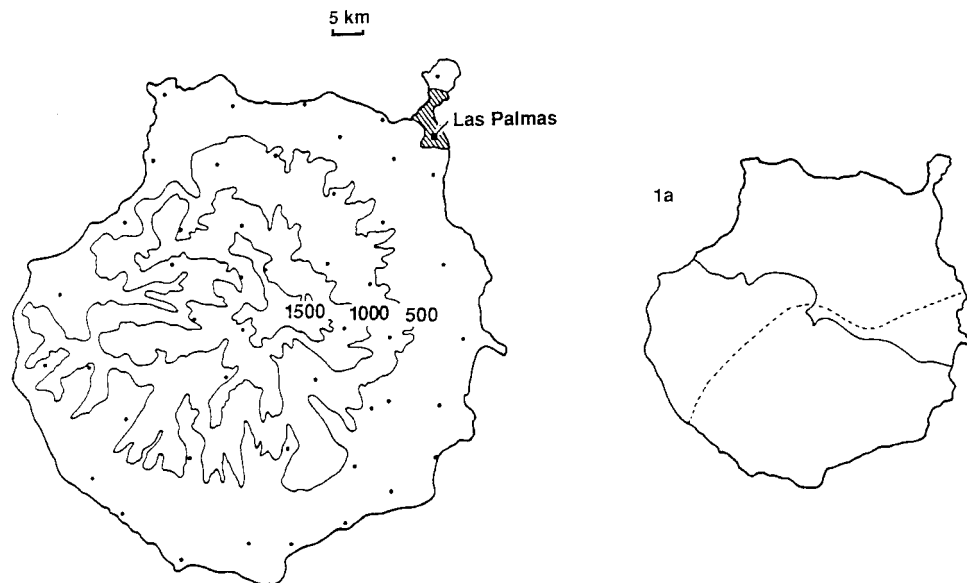


Fig. 1. Gran Canaria. *Chalcides sexlineatus* sample localities are represented by dots, altitude contours are in metres. a, the lush/arid ecotones and lush/arid ecotones plus gene flow hypotheses (unbroken line) and the two species hypothesis (broken line).

chin to the underside of the tail. Scores ranged from zero (no ventral orange pigment) to five (orange pigment on the whole of the ventral body surface and the underside of the tail); (C4) length and number of dorsal stripes. Minimum score was zero (no dorsal stripes) maximum score was four (dorsal stripes stretching the whole length of the body); (C5) number of ocellated scales in the central dorsal scale row, counting backwards from the head to the fore-limbs; (C6) size of light spot immediately anterior to the fore-limbs counted in number of scales; (C7) width of lateral dark band immediately anterior to the fore-limbs, counted in number of scales; (C8) extent of ventral black pigment. Black pigment spreads up the body from the underside of the tail up to the chin. Scores were from zero (no ventral black pigment) to four (black pigment extends to the chin).

The extent of the geographic variation in the dorsal colour pattern can be seen in Plate 1.

Analysis of Geographic Variation

For the numerical analyses, the sexes were separated (316 males; 375 females) so the word 'group' will be used to refer to all individuals of one sex collected from a particular locality. Spatial autocorrelation is unlikely in the data set because the locality spacing is greater than the dispersal range of *C. sexlineatus*.

Independence of individual characters was tested for using a pooled within-group product-moment correlation (see Thorpe, 1976; Thorpe, 1987). The presence of geographic variation and sexual dimorphism in colour pattern characters was tested for with two-way analyses of variance (ANOVA) on all the groups together. Congruence between patterns of geographic variation, (1) between characters within a sex, and (2) between sexes for each character, was tested for using product-moment correlations between mean group scores. Mean group character scores for each sex were converted to a 0 – 10 scale (representing the range of mean group scores) and then contoured using the Surface II algorithm (Sampson, 1978). This method gives a simple portrayal of the geographic variation using isophenes.

Canonical variate analyses (CVA) were computed on male and female groups separately to give generalized patterns of geographic variation. One advantage of CVA is that it takes into account any within-group covariance between characters when computing the among-group variation. Principal component analyses (PCA) were also run on the mean group character states (for male and female groups separately). The CVAs were then checked, in case they had been perturbed by heteroscedasticity, by correlating the PC1s with the group centroids for the CV1s (see Thorpe and Brown, 1989b). The first two canonical variates were contoured.

Hypothesis Testing

Four feasible hypotheses could explain the microgeographic variation in *C. sexlineatus*. Each hypothesis predicts a pattern of geographic variation.



Plate 1. Dorsal views of *C. sexlineatus* from; (A) the north-east of Gran Canaria showing uniform brown coloration and (B) the extreme south-west of the island showing 'striped' dorsum and bright blue tail coloration.

(i) *Hypotheses*

(1) Lush/arid ecotones hypothesis (Fig. 1A). The south of Gran Canaria experiences very little rainfall – data obtained from a weather station in Puerto Mogan (south-west coast) shows that an annual total of only 20.5 mm was recorded there in 1987. It is also generally hot and sunny – corresponding mean daily sunshine hours for Puerto Mogan was 8.43. In the north of the island, a greater abundance of cloud results in lower insolation – a weather station in Gula (north coast) gave mean daily sunshine hours of 5.31 for 1987. Also there is higher rainfall in the north – 196.2 mm rain in the same year. Corresponding to these climatic differences, there is a marked contrast in vegetation between northern and southern slopes of the island, the former being relatively lushly vegetated compared with the latter. A similar component of within-island variation in climate/vegetation is thought to be the primary cause of the geographic variation in the colour pattern of *G. galloti* on Tenerife (Thorpe and Brown, 1989a and b).

Areas of sharp vegetation change can be seen on a satellite photograph of the island (C.N.E.S. and Maptec Int. Ltd., 1987). This enables the localities in the lush north/north-east to be divided from those in the more arid south/south-west. For this hypothesis, localities above the line (i.e., in the north of the island) were scored 1, those below the line (south) 0.

(2) Lush/arid ecotones plus gene flow (Fig. 1A). This is the same hypothesis as that above but also incorporates a simple simulation of the effects of gene flow between populations in the northern and southern categories. This was done by scoring the localities according to their perpendicular distance from the lush/arid division line.

(3) Altitude hypothesis. Higher altitudes are much more seasonal than lower altitudes and also tend to experience a greater daily temperature range, e.g., weather stations gave figures for January, 1987, of 15.0° C and 9.0° C at Pinar de Tamadaba (altitude 1444 m) for mean daily maximum and minimum temperatures respectively, whereas for the neighbouring coastal area of Agaete, the corresponding figures were 22.7° C and 15.8° C. Coastal areas also tend to be more sparsely vegetated than middle/high altitude areas (Montelongo, Rodrigo and Bramwell, 1984). The scalation of both *C. sexlineatus* and *G. galloti* shows altitude-related geographic variation (Thorpe and Báez, 1987; Brown and Thorpe, 1990). For this hypothesis, the localities were scored by their height above sea-level in metres.

(4) Two species hypothesis (Fig. 1A). The fourth hypothesis originates from an attempt to relate the observed geographic variation to Pasteur et al.'s (1988) study, which proposed that two *Chalcides* 'species' with different ranges exist in Gran Canaria. Hence for this hypothesis, localities were scored either 1 or 0 according to whether they fell within either their proposed range of *C. sexlineatus* or within that of '*C. bistratus* species complex'.

(ii) *Partial correlation*

This tests the relationships between a dependent variable and several possible independent variables which may be statistically non-independent of one another (as in this case). It effectively computes correlations between the dependent variable

and each independent variable with the other independent variables held constant. Here, it is used to simultaneously test the four hypotheses (independent variables) against each described pattern of geographic variation (dependent variables). Twenty partial correlations were therefore computed on the four hypotheses, in which the described patterns were the group mean scores of each character and the first two canonical variates (for both sexes).

(iii) *Mantel tests*

Like partial correlation, these can also test between hypothesized causes of geographic variation and the observed pattern. The advantage of Mantel tests over partial correlation is that they can compare multidimensional matrices. This allowed comparison of the hypotheses with the entire colour pattern distance matrices (eight characters). The disadvantage is that no version is yet available that can simultaneously test more than three matrices.

Two types of Mantel tests were used (see Manly, 1986, and references therein). The first computes a measure of association between two matrices. This is expressed as a *G* statistic ($G = [Z - \text{Exp}]/\text{SE}$) which is then compared with the values of *G* given by random associations of the two matrices. We ran the test between the colour pattern distance matrices (males and females), computed using the eight characters, and each of the four hypotheses used in the partial correlation. The probabilities of the null hypotheses were calculated from the position of the actual *G* value in the range of *G* values produced by 500 random matrix associations.

The second type of Mantel tests used measures the association between three matrices. Here, we used it to compare two hypothesized matrices with the observed matrix. Five statistics are computed by this test; 1) a simple regression between the observed and the first hypothesized matrices (g_1), 2) a simple regression between the observed and the second hypothesized matrices (g_2), 3) a partial regression of the observed against the first hypothesized matrices with the effects of the second hypothesized matrix removed ($g_{1,2}$), 4) a partial regression of the observed against the second hypothesized matrices with the effects of the first hypothesized matrix removed ($g_{1,3}$), and 5) a multiple regression between the three matrices (R^2). The values of these statistics are then compared with the distributions of the same values given by random associations of the matrices.

Using Mantel 'three matrices' tests, we tested the colour pattern matrices (male and female) against, 1) the lush/arid ecotones and two species hypotheses, and 2) the lush/arid ecotones hypothesis and geographical proximity – computed from approximate latitude and longitude of the localities. Assuming that the extent of gene flow between populations is correlated to geographical proximity, the latter test indicates whether the lush/arid ecotones hypothesis is still significant after the effects of gene flow have been regressed out. For the 'three matrices' test, 100 random associations of the matrices were computed rather than the 500 associations computed for the 'two matrices' tests. This was because of the large amount of computer time taken to run these tests, and the fact that none of the results were of marginal significance in the third decimal place. Probabilities of the null hypotheses for each of the five statistics were calculated as for the two matrices test.

All Mantel tests were run using programs supplied by B. F. Manly which had been modified by R. S. Thorpe.

Results

Pattern of microgeographic variation

See Table 1. Pooled within-group correlations between characters were generally low (Table 2) implying that they represent independent units of genetic information (Thorpe, 1976). All eight characters showed significant among-locality variation but none were sexually dimorphic (Table 3). High product-moment correlations between group means (Table 4) indicate between-character congruence in the patterns of geographic variation (except C8) whilst high levels of congruence between the sexes for each character indicate that the described patterns are highly reliable.

Contoured patterns of microgeographic variation were similar for all characters except for C8 (Fig. 2). Characters C1–C7 show north-east/south-west clines with transition zones in the centre of the island. The inclination of the transition zones varies from very steep (e.g., C5), to more gradual (e.g., C1). In addition to a north-east/south-west cline, orange belly colour (C3) also shows an altitude-related pattern of microgeographic variation. Black belly colour (C8) shows a very different pattern of microgeographic variation to the other seven characters in that highest scores for this character are found in a small area of the west coast of the island,

Table 1. Summary statistics for the eight colour pattern characters. Maximum and minimum group means and pooled within-group standard deviations (S.D.) are given for each of the eight colour pattern characters for male (M) and female (F) groups.

Character		Minimum	Maximum	S.D
C1	M	0.00	5.00	0.61
	F	0.00	4.71	0.61
C2	M	0.00	3.71	0.60
	F	0.00	3.50	0.51
C3	M	0.54	4.75	0.71
	F	0.29	4.88	0.68
C4	M	0.71	4.00	0.53
	F	0.67	4.00	0.52
C5	M	0.00	17.00	2.87
	F	0.00	17.00	3.19
C6	M	0.00	4.80	1.00
	F	0.00	4.20	0.98
C7	M	3.14	9.44	0.99
	F	3.25	9.40	1.00
C8	M	0.00	3.63	0.56
	F	0.00	3.70	0.63

Table 2. Pooled within-group correlations between the eight colour pattern characters for male (M) and female (F) groups. Generally low correlation coefficients indicate that the characters represent independent facets of the phenotype (Thorpe, 1976).

		Characters							
		C1	C2	C3	C4	C5	C6	C7	C8
C1	M	–	0.38	0.05	0.10	0.17	–0.08	0.02	–0.21
	F	–	0.35	0.04	–0.05	–0.05	–0.02	0.02	–0.32
C2	M	–	–	0.00	0.06	0.15	0.04	–0.02	–0.10
	F	–	–	0.03	0.07	0.06	–0.02	0.00	–0.07
C3	M	–	–	–	0.00	0.00	0.05	–0.04	0.01
	F	–	–	–	0.00	0.06	0.01	–0.11	–0.03
C4	M	–	–	–	–	0.53	–0.03	0.02	–0.01
	F	–	–	–	–	0.51	0.06	0.01	0.01
C5	M	–	–	–	–	–	–0.07	0.02	–0.08
	F	–	–	–	–	–	0.02	0.09	0.05
C6	M	–	–	–	–	–	–	0.16	0.17
	F	–	–	–	–	–	–	0.20	0.03
C7	M	–	–	–	–	–	–	–	0.04
	F	–	–	–	–	–	–	–	0.03

Table 3. F ratio's from a two-way ANOVA for sexual dimorphism (Sex) and among-locality (Among-locality) variation in the eight colour pattern characters.

Character	Sex	Among-locality
C1	0.00	87.32
C2	0.00	90.76
C3	1.56	82.45
C4	0.05	82.45
C5	0.14	70.97
C6	0.30	35.55
C7	1.07	63.77
C8	1.16	19.46

For sex, $P > 0.05$ for each character. For among-locality variation, $P < 0.001$ for each character.

medium scores on the small peninsula in the extreme north-west of the island and lowest scores in all other parts of the island.

CVA shows that the geographic variation in colour pattern is largely unidimensional, i.e., most of the among-group variation is expressed by the first canonical variates (males, 72.3%; females 77.8%). CV1s were correlated with PC1s for both males ($r = 1.0$) and females ($r = 0.99$). CV1s and PC1s therefore gave the same pattern of among-group variation, so future references to generalized microgeographic variation will be to the CVA.

Contouring of the generalized microgeographic variation (Fig. 3) shows north-east/south-west stepped clines. The highest CV1 scores were on the middle-high

Table 4. Between-sex (BS) and between-character correlations (M, male and F, female) based on the group means of the eight colour pattern characters. $P < 0.001$ for all of the between-sex correlations indicating that the numerically described patterns are reliable. $P < 0.001$ for all of the between-character correlations except for those with C8 (where $P > 0.05$ in each case) indicating that the geographic variation in colour pattern is largely unidimensional.

		Colour pattern characters							
		C1	C2	C3	C4	C5	C6	C7	C8
C1;	M	–	0.934	–0.516	0.825	0.832	–0.739	–0.624	–0.032
	F	–	0.915	–0.521	0.880	0.904	–0.746	0.670	0.016
	BS	0.972							
C2;	M		–	–0.555	0.896	0.922	–0.797	–0.679	–0.003
	F		–	–0.578	0.871	0.925	–0.743	–0.626	0.027
	BS		0.962						
C3;	M			–	–0.714	–0.600	0.689	0.769	–0.176
	F			–	–0.686	–0.591	0.753	0.756	–0.096
	BS			0.907					
C4;	M				–	0.933	–0.914	–0.824	0.036
	F				–	0.936	–0.887	–0.805	0.116
	BS				0.971				
C5;	M					–	–0.815	–0.710	–0.071
	F					–	–0.780	–0.715	0.011
	BS					0.976			
C6;	M						–	0.881	–0.155
	F						–	0.868	–0.287
	BS						0.936		
C7;	M							–	–0.068
	F							–	–0.096
	BS							0.966	
C8;	M								–
	F								–
	BS								0.824

altitude northern slopes of the island, lowest scores in the coastal and inland SW area of the island. Some altitude-related microgeographic variation can be seen in CV2 (Fig. 3).

Hypothesis Testing

(i) Partial correlation (Table 5)

Of the twenty partial correlation analyses, fourteen do not reject the lush/arid ecotones hypothesis as a cause of the geographic variation, i.e., for characters C1, C2, C4, C5, C6 and C7 (males and females), and the generalized geographic variation, (CV1, males and females).

Table 5. Partial correlations between the four hypotheses and the colour pattern characters and canonical variates for male (M) and female (F) groups. LA is the lush/arid ecotones hypothesis, LA + G is the lush/arid ecotones plus gene flow hypothesis.

Characters/ canonical variates		Hypotheses			
		Altitude	LA	LA + G	Two species
C1	M	-0.075	-0.429**	-0.438**	0.435**
	F	-0.127	-0.449**	-0.489***	0.440**
C2	M	0.112	-0.431**	-0.356*	0.250
	F	0.043	-0.414**	-0.332*	0.237
C3	M	0.500***	0.157	0.336*	0.083
	F	0.468**	0.126	0.333*	0.170
C4	M	0.073	-0.559***	-0.466**	0.277
	F	0.050	-0.644***	-0.401**	0.299
C5	M	0.153	-0.566***	-0.236	0.141
	F	0.054	-0.554***	-0.212	0.157
C6	M	-0.029	0.488***	0.353*	-0.226
	F	-0.066	0.308*	0.359*	-0.097
C7	M	0.072	0.325*	0.406**	0.130
	F	0.127	0.370*	0.311*	0.127
C8	M	-0.024	0.099	-0.074	0.106
	F	-0.091	-0.153	0.044	0.332*
CV1	M	0.013	0.347*	0.380**	0.016
	F	0.049	0.455**	0.213	-0.133
CV2	M	0.212	-0.165	0.040	0.302*
	F	0.202	-0.116	0.000	0.213

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

The lush/arid ecotones plus gene flow hypothesis is not rejected as a cause of the geographic variation in characters C1, C2, C3, C4, C6 and C7 (males and females) or the generalized male geographic variation.

The altitude hypothesis is rejected by all of the partial correlations except for C3 ($P < 0.001$ for males and females). Similarly, the two species hypothesis is rejected except for two of the characters, C1 and C8, the latter being significant for female groups only.

(ii) 'Two matrices' Mantel tests (Table 6)

In the eight 'two matrices' Mantel tests, only the altitude hypothesis is rejected as a possible cause of the geographic variation in the colour pattern (for both sexes).

(iii) 'Three matrices' Mantel tests (Table 7)

The 'three matrices' tests do not reject the lush/arid ecotones hypothesis as a cause of the geographic variation in colour pattern for either males or females. Furthermore, this hypothesis remains significant when the effects of either the two

Table 6. Mantel 'two matrices' tests between the colour pattern distance matrices and the altitude, Lush/arid ecotones (LA), lush/arid ecotones plus gene flow (LA + G), and two species hypotheses. The probabilities of the null hypotheses (*P*) are from the position of the actual *G* value (*G*) in relation to the values obtained from 500 random associations of the matrices.

Colour pattern matrix	Hypothesis	<i>G</i>	<i>P</i>
Male	Altitude	0.271	0.332
Female	Altitude	0.555	0.286
Male	LA	19.992	0.000
Female	LA	19.924	0.000
Male	LA + G	10.882	0.000
Female	LA + G	13.072	0.000
Male	Two species	7.980	0.000
Female	Two species	8.854	0.000

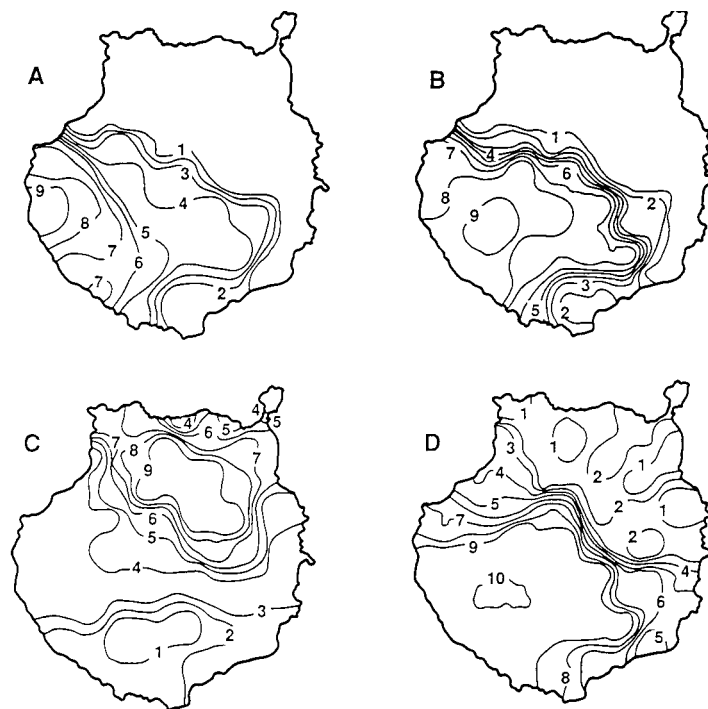


Fig. 2.

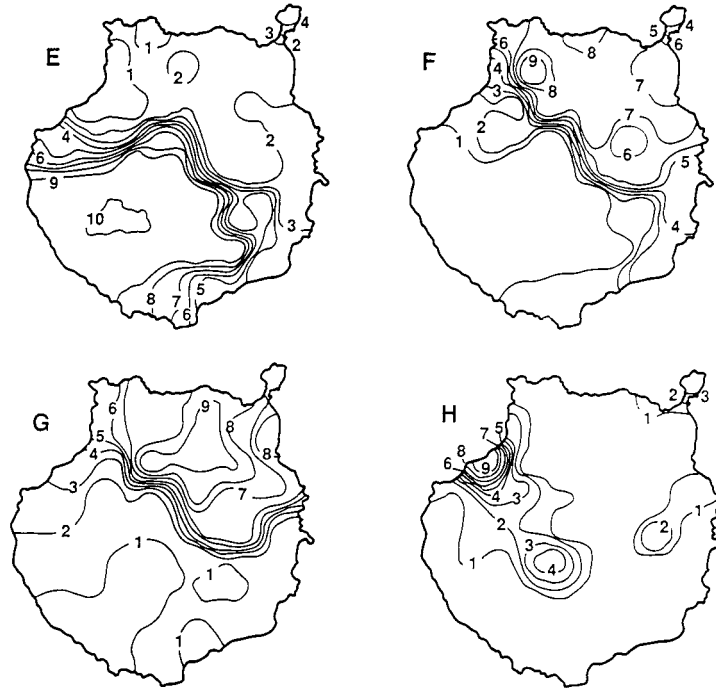


Fig. 2. Contours portraying the geographic variation among the male group means of the individual colour pattern characters. The means were scaled on a 0 to 10 range (Table 1). A, extent of ventral blue pigment up the belly (C1); B, dorsal tail colour (C2); C, extent of orange pigment down the tail/belly (C3); D, length and number of dorsal stripes (C4); E, number of dorsal ocellated scales (C5); F, size of light spot on shoulder (C6); G, width of lateral dark band at the shoulder (C7); H, extent of black pigment up the tail/belly (C8).

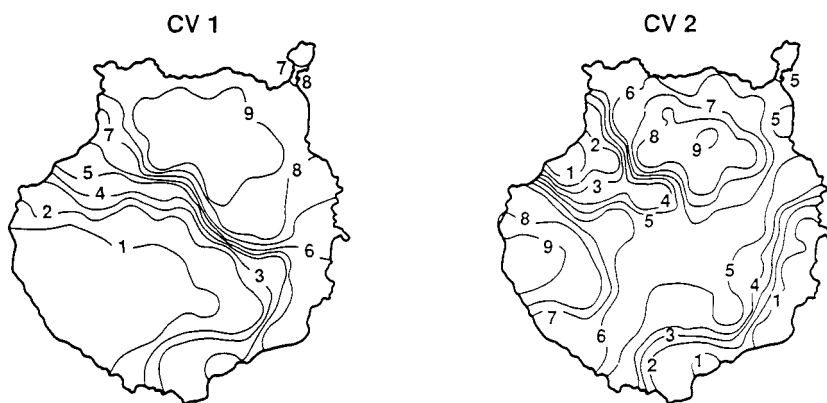


Fig. 3. Contours portraying the geographic variation in the first and second canonical variates (based on male group mean scores and scaled on a 0 to 10 range).

Table 7. Mantel's 'three matrices' tests. Male and female colour pattern matrices were tested against the lush/arid ecotones and two species (LA, 2SP) hypotheses, and against the lush/arid ecotones hypothesis and geographical proximity (LA, PRX). The lush/arid ecotones was the first hypothesized matrix in each test. The test computes five measures of association of the matrices: A simple regression between the observed and the first hypothesized matrices (g_1); a simple regression between the observed and the second hypothesized matrix (g_2); a partial regression between the observed and first hypothesized matrices with the effects of the second hypothesized matrix regressed out ($g_{1,2}$); a partial regression between the observed and second hypothesized matrices with the effects of the second hypothesized matrices regressed out ($g_{1,3}$); a multiple regression (R^2). Each of these measures of association was compared with the distribution of their values given by 100 random associations of the matrices. This gave the probabilities.

Matrices		Measures of association				
Observed	Hypothesized	g_1	g_2	$g_{1,2}$	$g_{1,3}$	R^2
Male	LA, 2SP	0.361*	0.157*	0.367*	-0.012	0.348*
Female	LA, 2SP	0.360*	0.172*	0.355*	0.011	0.344*
Male	LA, PRX	0.361*	0.274*	0.300*	0.157*	0.403*
Female	LA, PRX	0.360*	0.277*	0.297*	0.161*	0.401*

* $P < 0.01$.

species hypothesis or geographical proximity are removed (i.e., the measure of association given as $g_{1,2}$ in Table 7).

Discussion

Most aspects of the colour pattern of *C. sexlineatus* show north-east/south-west patterns of microgeographic variation. This overall trend bears close similarity to the patterns of microgeographic variation in the body dimensions and scalation of the same species (Brown and Thorpe, 1990). Moreover, a parallel latitudinal pattern of microgeographic variation is found in the colour pattern (Thorpe and Brown, 1989a and b), and to some extent the scalation (Thorpe and Báez, 1987), of the lizard *Galloti galloti* on the neighbouring island of Tenerife.

Of the four hypotheses proposed to explain the geographic variation in colour pattern, partial correlation shows that only the two lush/arid ecotones hypotheses are pertinent. The two species hypothesis is rejected as a cause of the geographic variation in most of the characters and the overall colour pattern. However, although the method of hypothesis testing used in this study can demonstrate that the ranges of the putative species are wrong, it cannot fully discount the possibility that two species are present. This possibility is rejected on other criteria; the presence of the north-south transition zone containing localities with intermediate mean character states clearly runs counter to the two species proposal. Furthermore, close analysis of the scalation characters, on which Pasteur et al. based their designation, does not support the idea of two reproductively isolated entities (Brown and Thorpe, 1990).

Partial correlation is clearly the most effective method of numerically testing the hypotheses because it removes the intercorrelation between them. This is despite two drawbacks, namely that the 1, 0 distributions of two of the hypotheses may affect the confidence limits, and that it is limited to unidimensional comparisons. Mantel 'two matrices' tests do not discriminate between the intercorrelated patterns of three of the hypotheses, indicating the importance of a simultaneous hypothesis testing approach. The simultaneous 'three matrices' test is more useful in our study as it is able to discriminate between the two species and the lush/arid ecotones hypotheses. It also enables the removal of geographic proximity from the hypotheses, which is not a unidimensional effect and therefore cannot be included in the partial correlations.

Lush/arid ecotone changes, broadly similar to those in Gran Canaria, also occur in Tenerife which appears to cause differential selection on the colour pattern of adult male *G. galloti* (Thorpe and Brown, 1989a and b). A consideration of the possible selective factors causing the microgeographic variation in *C. sexlineatus* is useful in view of the parallel patterns of microevolution between these two species. In *G. galloti* the within-island variation in climate and vegetation appears to influence a trade-off between selection for aspects of the colour pattern which enhance sexual attractiveness, and for those which enhance crypsis. Such a trade-off has previously been described in guppies (Endler, 1978, 1980 and 1983) and occurs when sexual attractiveness increases conspicuousness to predators.

The lack of sexual dimorphism in any of the characters used shows that the colour pattern of *C. sexlineatus* is not determined by sexual selection. Unlike many other lizard species therefore, the colour pattern of this species apparently does not function in sex recognition. Lack of sexual dimorphism in colour pattern also means that the *G. galloti* 'crypsis versus sexual advertisement' hypothesis is not appropriate. However, like male *G. galloti*, *C. sexlineatus* does have a cryptic dorsal coloration in the north of the island. This indicates that there is a high premium on remaining unseen by aerial predators, such as *Falco tinnunculus*, which prey upon *C. sexlineatus* in both the north and the south of Gran Canaria (F. Rodriguez, unpubl. data) as well as *G. galloti* on Tenerife.

In contrast to the cryptic coloration in the north of the island, individuals of *C. sexlineatus* from the central/south-west of Gran Canaria have a conspicuous blue/green tail coloration. This is thought to be an anti-predator adaptation in lizards; studies on skinks of the genus *Eumeces* have shown that predators direct their attack towards conspicuously coloured tails which can then autotomize, allowing the skink to escape (Cooper and Vitt, 1985; Vitt and Cooper, 1986). A possible disadvantage of this strategy is that the bright colour of the tail may enhance the predator's ability to detect the skink.

We propose two possible mechanisms for the evolution of the conspicuous tail and the cryptic colour patterns on Gran Canaria; (1) lower temperatures and greater cloud cover in the north could force the skinks to spend long periods basking in order to reach their preferred body temperatures. The cost associated with basking is that the skink is exposed to predators when it is most vulnerable due to sub-optimal body temperatures. Flight-escape efficiency will be reduced at

these lower body temperatures so avoidance of detection (i.e., crypsis) is the best strategy. *G. galloti* shows cryptic coloration in the north of Tenerife where climatic conditions parallel those in Gran Canaria – this is also thought to be associated with a longer warm-up period (Thorpe and Brown, 1990). In the south of the island, where cloud cover is much lower and temperatures higher, the skinks spend less time at lower body temperatures which favours a flight-escape strategy over a cryptic one. The bright blue tail coloration could have evolved to complement the flight-escape anti-predator strategy by serving to displace a pursuing predator's attack towards the expendable tail of a fleeing lizard. Thus the two strategies could have arisen via different climate-determined thermoregulation patterns. Hertz et al. (1982) have shown a change in anti-predator behaviour correlated with body temperature in an agamid lizard. (2) Greater vegetation cover in the north could increase the effectiveness of a cryptic strategy whilst the sparse vegetation cover in the south could favour a strategy involving conspicuous tail coloration. Arnold (1984) reviews the occurrence of conspicuous tail coloration in some Old World lizards and finds that it is most common in species that habitually occur in open habitats, whereas brightly coloured tails tend to be absent in lizards that are found in densely vegetated habitats. He concludes that lizards living in open, uniform habitats are quite easily seen even when their dorsal coloration matches that of the background so cryptic strategies are unlikely to be effective. Thus the two strategies could have arisen from the differences in vegetation cover between the north and the south of the island.

The two proposed mechanisms for the microevolution of the colour pattern are not mutually exclusive, the climate and vegetation-determined selection pressures could act together in an additive manner.

The microgeographic variation in other colour pattern characteristics of *C. sexlineatus*, are less easy to explain. Orange pigment is found on the heads of several skink species, especially species of the genus *Eumeces*. In *Eumeces laticeps* the pigment is a sexually selected character that serves to identify the bearer as a male (Cooper and Vitt, 1988). The orange pigment appears to have a different function in *C. sexlineatus* as it is ventrally distributed and not sexually dimorphic. It could function in intra-specific communication as individuals from most parts of the island show some orange coloration in the throat area (where it would be visible to conspecifics). In northern areas, where some individuals carry the pigment on the whole of the ventral surface, the function is more likely to be that of anti-predator flash coloration. The pigment would normally remain unseen (being on the underside) but could serve to startle a predator if the skink was captured. Several amphibians show bright belly coloration which they display when under the threat of attack (e.g., *Bombina*). The extent of the orange pigment is also closely related to altitude as are the number of body scales of the same species (Brown and Thorpe, 1990) and the scalation of *G. galloti* on Tenerife (Thorpe and Báez, 1987).

Blue ventral pigment is found only on individuals from southern parts of the island and extends from the cloaca up to the chin in animals from the extreme south-west. This could, like the orange pigment, also serve as flash coloration. Lateral colour pattern characters could function in intra-specific communication as they are situated on the animals flanks.

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