

# Parallel within-island microevolution of lizards on neighbouring islands

R. P. Brown\*†, R. S. Thorpe\* & M. Báez‡

\* Zoology Department, University of Aberdeen, Aberdeen AB9 2TN, UK

‡ Departamento de Zoología, Facultad de Biología,

Universidad de La Laguna, La Laguna, Tenerife, Canary Islands, Spain

**THE correlation of changes in morphological traits with environmental gradients is often taken as evidence for natural selection<sup>1</sup>. But in many cases, the possibility that this correlation is coincidental cannot be ruled out<sup>2</sup>. Stronger evidence for natural selection is provided when closely related allopatric species show parallel patterns of geographic variation along similar environmental gradients. Vertebrate geographic variation within small islands provides a valuable opportunity to detect mechanisms of natural selection<sup>3-5</sup>. We have now studied microgeographic variation in the colour patterns of two skinks (Lacertilia: Scincidae) from neighbouring heterogeneous islands. Parallel north-south variation occurs in the colour patterns of both species. Populations from the south of both islands possess conspicuous dorsal-tail coloration. Morphological distance matrices for both species are compared with similar aspects of environmental variation using simultaneous Mantel tests. This indicates that differential selection between lush and arid habitats is the primary cause of the variation in colour pattern.**

*Chalcides sexlineatus* is endemic to the Canary Island of Gran Canaria (Spain) where it shows within-island geographic variation in several morphological characteristics<sup>6,7</sup>. The sister species *Chalcides viridanus* is present on the adjacent island of Tenerife. The colour patterns of 432 *C. viridanus* from 17 localities within Tenerife and 691 *C. sexlineatus* from 47 localities in Gran Canaria were recorded using macrophotography.

Four unit characters quantified the main features of the colour-pattern variation in *C. viridanus*: (1) number of dorsal ocelli; (2) blue tail coloration; (3) green tail coloration; (4) dorsal hue. The first two of these characters could take several different values. Two-way analyses of variance (ANOVA) showed that they varied significantly between localities ( $F = 4.48$ ,  $P < 0.001$ ;  $F = 35.81$ ,  $P < 0.001$ , respectively) and between adult and juvenile age classes ( $F = 4.48$ ,  $P < 0.02$ ;  $F = 54.98$ ,  $P < 0.001$ , respectively); a logarithmic transformation of the character value, did not affect these probabilities). The other two characters are either present or not, and their values were not the same between the localities for adults (Pearson  $\chi^2$  are 130.46 and 82.76,  $P < 0.001$ , respectively). The values of these characters were invariant for juveniles. A principal components analysis (PCA) was computed on the normalized group-means of the values of the four adult character to give the generalized geographic variation in colour pattern<sup>8</sup>. The variation is predominantly from north to south (Fig. 1a).

Eight different continuous characters were used to quantify the main features of the colour-pattern variation in *C. sexlineatus*: (1) blue belly pigment; (2) blue dorsal-tail coloration; (3) orange belly pigment; (4) dorsal stripes; (5) number of dorsal ocelli; (6) size of light shoulder blotch; (7) size of lateral dark band at shoulder; (8) ventral black pigment. Two-way ANOVAs showed that the values of the characters vary significantly among localities ( $F$  values, respectively: 87.32; 90.76; 37.59; 82.45; 70.97; 35.55; 63.77; 19.56;  $P < 0.001$  for all), but are not sexually dimorphic ( $P > 0.05$  for all). A logarithmic transformation of the character value did not affect these probabilities. Canonical

TABLE 1 Variable coefficients for the first canonical variates (*C. sexlineatus*)

	Colour-pattern characters							
	1	2	3	4	5	6	7	8
Males	-0.59	-0.55	0.45	-0.67	-0.07	0.26	0.42	-0.39
Females	-0.71	-0.68	0.52	-0.72	-0.08	0.24	0.41	-0.29

All characters show substantial loadings on the first canonical variates (except character 5). For *C. viridanus*, normalized eigenvector coefficients for the first principal component were 0.55, -0.62, 0.01 and 0.56 for characters 1, 2, 3 and 4, respectively. The rationale for computing canonical variates and principal components analyses was that they condense most of the among-locality variation into (in this case) a single vector which can then be conveniently portrayed using a contouring program (Fig. 1).

variate analyses (CVA) computed for the eight characters condensed most of the between-group variation in *C. sexlineatus* (males, 72.3%; females 77.8%) into one measure of colour-pattern variation, that is, the first canonical variate (Table 1) (the results were checked using PCA to ensure that heteroscedasticity had not perturbed the CVA<sup>3,9</sup>). This variable shows a clear NNE-SSW pattern of geographic variation (Fig. 1b).

Three hypotheses could explain the colour-pattern variation in *C. sexlineatus* on Gran Canaria, whereas two hypotheses are feasible for *C. viridanus* on Tenerife. These are:

■ **Lush/arid habitats hypothesis** (*C. viridanus* and *C. sexlineatus*, Fig. 2). There are pronounced differences in climate and vegetation between the north and south of both Tenerife and Gran Canaria. These seem to be the primary cause of geographic variation in other lizard species on the former island<sup>3,4,5</sup>. The categorical nature of the lush-arid variation allows the use of a dual-state variable for hypothesis testing.

■ **Altitude hypothesis** (*C. sexlineatus* only; *C. viridanus* is a predominantly low-altitude species). Gran Canaria reaches a height of 1,949 m, giving rise to altitude-related variation in climate and vegetation<sup>10,11</sup>. The scalation of several species of lizards has been shown to covary with altitude<sup>4,6</sup>. Localities were therefore scored according to their height above sea level.

■ **Geographical proximity hypothesis** (*C. viridanus* and *C. sexlineatus*), which models gene flow according to an isolation-by-distance model<sup>12</sup>.

A two-hypothesis simultaneous Mantel test was used to test the models<sup>13</sup>. The colour-pattern distance matrix for each species consisted of the mean population scores for all colour characters ('observed' matrices). The two 'hypothesized' matrices represented the lush/arid habitats hypothesis or altitude hypothesis in addition to the geographical-proximity hypothesis.

The lush/arid habitats hypothesis is significant for both adult and juvenile *C. viridanus* (Table 2). For male and female *C. sexlineatus*, the lush/arid habitats hypothesis is significant and remains so after the removal of geographical proximity. The altitude hypothesis is rejected.

These findings indicate that the lush/arid changes in climate and vegetation within the islands may determine natural selection for different colour-pattern morphs. Possibly the most interesting aspect of the variation is the presence of a conspicuous blue-green dorsal-tail coloration in animals from the arid southern areas of both of the islands. This could be an adaptive response to predation pressure from kestrels (*Falco tinnunculus*) and perhaps shrikes (*Lanius excubitor*). Tail autotomy, the ability to shed the tail when attacked, is a well-known anti-predator device in lizards<sup>14</sup>, the effectiveness of which may be increased by conspicuous tail coloration<sup>15</sup>. Skinks from the north of both islands have generally dark, uniform, cryptic dorsal colour patterns. It seems likely that these morphs represent alternative anti-predator strategies which have arisen by the different selective pressures that exist between lush and arid habitats. Different predator escape strategies could be favoured in different habitats<sup>14</sup> (that is crypsis versus conspicuous tail strategies). Alternatively, the shrike is thought to be more abundant in arid habitats, which could reflect geographic variation in predation pressure. □

† Present address: Departamento de Zoología, Facultad de Biología, Universidad de Salamanca, 37071 Salamanca, Spain.

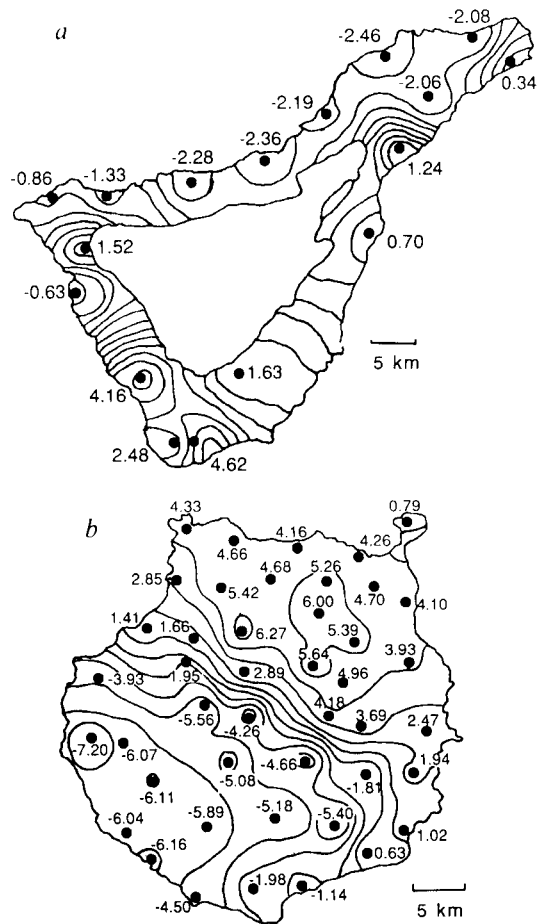


FIG. 1 Patterns of geographic variation in coloration. *a*, Contour plot of the first principal component representing 58.3% of total among-population variation in *C. viridanus* in Tenerife (the blank centre is the area of 'absence'). *b*, The same for female *C. sexlineatus* on Gran Canaria (first canonical variate representing 77.8% of total among-population variation).

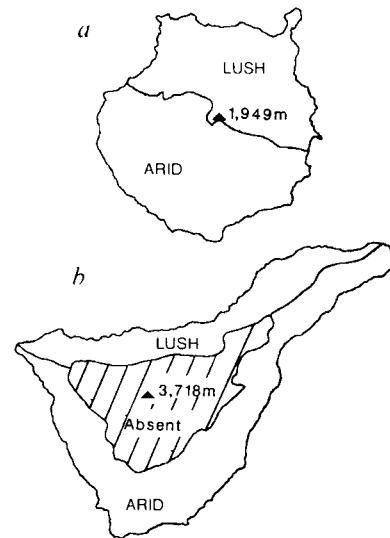


FIG. 2 Lush/arid habitat/hypothesis modelling habitat variation within the islands. The island's topography and the prevailing north/north-east trade winds, result in cloud formation on the north-facing slopes<sup>10,11</sup>. By contrast, the south of the islands are generally cloud-free, exhibiting higher temperatures and lower rainfall. These latitudinal climatic transitions are pronounced and give rise to corresponding changes in vegetation. For example, the original extent of the luxuriant laurisilva forest coincides with areas of semi-permanent cloud cover on the north-facing slopes<sup>16,11</sup>. Vegetation cover in the south is extremely sparse, consisting of xerophytic plants. Well-defined ecotones separate 'lush' and 'arid' biotopes, the exact location of which were determined by aerial photographs of the islands (see, for example, ref. 17). *a*, Gran Canaria. *b*, Tenerife. (Note that *C. viridanus* seems to be absent or only present at extremely low population densities above 1,100 m on Tenerife, so this part of the island (hatched) was not included when calculating the hypotheses distance matrices.)

TABLE 2 Mantel tests

Colour-pattern matrix (1)	Hypothesized matrices		$g_{1,2}$	$g_{1,3}$	$g_{1,2-3}$	$R^2$
	(2)	(3)				
<i>C. viridanus</i> (juveniles)	Lush/arid habitats	Geographical proximity	0.142 **	0.269 ***	0.117 *	0.142 **
<i>C. viridanus</i> (adults)	Lush/arid habitats	Geographical proximity	0.164 **	0.259 ***	0.141 **	0.219 ***
<i>C. sexlineatus</i> (males)	Lush/arid habitats	Geographical proximity	0.368 ***	0.276 ***	0.307 ***	0.411 ***
<i>C. sexlineatus</i> (females)	Lush/arid habitats	Geographical proximity	0.360 ***	0.274 ***	0.296 ***	0.400 ***
<i>C. sexlineatus</i> (males)	Altitude	Geographical proximity	0.011 NS	0.274 ***	0.056 NS	0.243 ***
<i>C. sexlineatus</i> (females)	Altitude	Geographical proximity	0.004 NS	0.277 ***	0.052 NS	0.261 ***

The five statistics computed by the Mantel tests are (1) a simple regression ( $g_{1,2}$ ) between the second hypothesized and the observed matrices, (2) a simple regression ( $g_{1,3}$ ) between the second hypothesized and the observed matrices; (3) a partial regression ( $g_{1,2-3}$ ), of the observed against the first hypothesized matrices with the effects of the second hypothesized matrix (proximity) removed; (4) a squared multiple correlation ( $R^2$ ). The values for these statistics are then compared with the ranges of values for the same statistics given by 500 random associations of the matrices. \* $P < 0.1$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.002$ ; NS (not significant),  $P > 0.1$ .

Received 28 January; accepted 13 May 1991.

1. Endler, J. A. *Geographic Variation, Speciation and Clines* (Princeton University Press, Princeton, New Jersey, 1977).
2. Endler, J. A. *Natural Selection in the Wild* (Princeton University Press, Princeton, New Jersey, 1986).
3. Thorpe, R. S. *Syst. Zool.* (in the press).
4. Thorpe, R. S. & Báez, M. *Evolution* **41**, 256-268 (1987).
5. Thorpe, R. S. & Brown, R. P. *Biol. J. Linn. Soc.* **38**, 303-322 (1989).
6. Brown, R. P. & Thorpe, R. S. *Biol. J. Linn. Soc.* (in the press).
7. Brown, R. P. & Thorpe, R. S. *J. Evol. Biol.* (in the press).
8. Thorpe, R. S. *Biol. J. Linn. Soc.* **14**, 215-233 (1980).
9. Thorpe, R. S. in *Numerical Taxonomy* (ed. Felstein, J.) 404-423 (NATO Advanced Study Institute Series G (Ecological Sciences), No. 1. Springer-Verlag, Berlin, 1983).

10. Fernandopulle, D. in *Biogeography and Ecology of the Canary Islands* (ed. Kunkel, G.) 185-206 (Junk, The Hague, The Netherlands, 1976).
11. Garcia, J. L. Hernández, J. Cabrera, L. G. Diaz, A. & Afonso L. *Atlas Interinsular de Canarias* (Editorial Interinsular Canaria, S.A. Tenerife, Spain, 1990).
12. Douglas, M. E. & Endler, J. A. *J. theor. Biol.* **99**, 777-795 (1982).
13. Manly, B. F. J. *Res. Pop. Ecol.* **28**, 201-218 (1986).
14. Arnold, E. N. *J. Nat. Hist.* **18**, 127-169 (1984).
15. Cooper, W. E. & Vitt, L. J. *Z. Tierpsychol.* **70**, 265-276 (1986).
16. Kammer, F. *Scripta Geobotanica* **7**, 1-78 (1974).
17. C.N.E.S. & Maptec Int. Ltd. *Imagen Satellite: Gran Canaria* (CNES Quaestus Int. Ltd. (dist.), Dublin, Ireland, 1987).

ACKNOWLEDGEMENTS. This research was funded by the Natural Environment Research Council (R.P.B.), Carnegie Trust (R.S.T.) and the British Council (R.S.T. and M.B.).