Evolution, 50(2), 1996, pp. 524–531

THE USE OF DNA DIVERGENCE TO HELP DETERMINE THE CORRELATES OF EVOLUTION OF MORPHOLOGICAL CHARACTERS

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Abstract.—Even though, from Darwin onwards, interisland evolution has been a cornerstone of evolutionary theory it has not been possible to determine to what extent this geographic variation reflects the phylogeny (e.g., pattern of island colonization) or ecogenetic adaptation to different ecological conditions on each island. Using the morphology of western Canary Island lacertids (*Gallotia galloti*) as an example, a procedure is explored that gives a preliminary answer to this problem when there are a limited number of islands. The phylogenetic component (represented by patristic distances derived from 1005 mitochondrial DNA [mtDNA] base pairs) can be separated from two potential ecogenetic factors (environmental richness and climate) by partial Mantel tests. This reveals that, although these components interact, some characters are correlated primarily to biodiversity/paucity (e.g., size), others are correlated to wet and lush environments (e.g., dorsal pattern), and others are correlated primarily to the phylogeny (e.g., sexual leg markings). The former two correlations may be due to ecogenetic adaptation to current ecological conditions, wheras the latter reflects historical processes.

Key words.—Canary Island lizards, ecogenesis, geographic variation, island evolution, morphology, mtDNA sequence, natural selection, partial Mantel tests, phylogenesis, phylogeography, selective neutrality.

Received April 1, 1994. Accepted March 8, 1995.

In spite of the substantial literature on interisland evolution in morphology since Darwin's (1859) Galápagos studies, and its influence on evolutionary theory (Mayr 1963; Berry 1992), there has been little rigorous attempt to determine the relative importance of the historical, phylogenetically inherited effect (e.g., the influence of the sequence of island colonization) and the effect of natural selection for current ecological conditions on different islands. This is all the more notable in light of the development of the "comparative method" to establish adaptation in traits by taking into account the phylogenetic relationships among species (Felsenstein 1985; Cheverud et al. 1985; Brooks and McLennan 1991; Harvey and Pagel 1991; Gittleman and Luh 1992; Losos 1990: Garland et al. 1991).

The "comparative method" has been applied primarily to comparisons among species (Richman and Price 1992), whereas interisland evolution is often studied at the level of intraspecific geographic variation. Although spatial (Cliff and Ord 1981) and "comparative" (Cheverud et al. 1985; Gittleman and Kot 1990) autoregression methods are related, intra- and interspecific traditions of data analysis have developed largely independently. Consequently, whereas independent contrasts (Felsenstein 1985) are important in interspecific studies, Mantel tests and their extensions, partial Mantel tests, are one of the main hypothesis testing techniques in geographic variation analysis (Manly 1991; Brown et al. 1991; Sokal et al. 1991; Smouse and Long 1992 and references therein; Thorpe 1991; Thorpe et al. 1994a and references therein; Waddle 1994).

Mantel tests are used to test one or more hypotheses (independent variables represented as matrices) against an observed pattern (dependant matrix) using (partial) regression or correlation. In geographic variation studies, a pattern of relative dissimilarities in morphology may be tested against one or more putative causal factors such as geographic variation in environmental conditions and or the opportunity for gene flow (Brown et al. 1991). They may also be used to test historical hypotheses derived from morphological data (Thorpe et al. 1994a; Waddle 1994) or from DNA phylogenies (Daltry et al. 1996; Thorpe et al. 1995). An example of the latter was given in Thorpe et al. (1995) where the DNA phylogeny (represented as a matrix of patristic distances among localities) of numerous lizard populations on a single island is tested against patterns generated from alternative historical hypotheses. This suggested that the single island currently occupied by the lizard was once composed of two separate precursor islands with preexisting lizard populations, which met once the precursors were joined into a single island by intervening volcanic activity.

Moreover, in intraspecific studies, molecular phylogenetic relationships may be incorporated into a partial Mantel test to test whether features are significantly associated with ecological factors (implying ecogenetic adaptation by natural selection) free of phylogenetic effects. Thorpe et al. (1995) gave two examples of this. The first example is an extension of the above island lizard study; a partial Mantel test was used to test observed color-pattern variation simultaneously against geographic proximity, patristic distances from the molecular phylogeny and a pattern generated by hypothesized ecogenetic adaptation to climatic/vegetational biotopes. This allowed the association between color pattern and biotopes to be established with the phylogeny partialed out. The results were supported by separate Mantel tests, of color pattern against biotopes and proximity, within each phylogenetic lineage (Thorpe at al. 1995; Thorpe et al., in press). The second intraspecific example (Thorpe et al. 1995; Daltry et al. 1996) used a partial Mantel test to establish an association between venom variation and diet, with phylogenetic effects partialed out, by simultaneously testing venom against diet, patristic distances from molecular phylogeny, and geographic proximity. The association between venom and diet free of phylogeny was confirmed by independent contrasts (Daltry et al. 1996).

Although it was possible to use independent contrasts after appropriate manipulation of venom and diet data, Mantel tests have clear advantages with these intraspecific examples. When dealing with intraspecific geographic variation adjacent populations may be able to exchange genes, and there may be unspecified geographic effects, so it is useful to consider gene flow/geographic proximity in two-dimensional space, and this is essentially matrix in form. This matrix form can be input directly into a Mantel tests but is inappropriate for independent contrasts. It is also useful to test "generalized" data sets combining several characters into a single matrix. In the above examples (Thorpe et al. 1995) generalized diet, generalized venom, and generalized color pattern are all matrices representing several characters. Vectors (principal components/coordinates) may be extracted to give a continuous variable representing these sets for input into independent contrasts, but information is lost in this process.

At the intraspecific level, it is quite usual for some pairs of populations not to be phylogenetically different, even though they differ in other dependent variables (e.g., ecology) and in the dependent variables (e.g., morphology), and hence should be included in the analysis (Thorpe et al. 1995). These data present no difficulty for Mantel tests but is inappropriate for independent contrasts. Nonnormal data are also acceptable for Mantel tests that are based on randomization.

In studies of geographic variation, it can be important to consider simultaneously several causative factors. This is done automatically in partial Mantel tests but cannot be achieved by independent contrast analysis on its own (requiring input of contrast traits into an additional analysis). Finally, independent contrasts do not consider variation among individuals, although this can be pertinent in studies of geographic variation where both descriptive methods such as principal-component analysis and canonical analysis (Thorpe 1983) and hypothesis testing methods such as Mantel tests (Excoffier and Smouse 1994; Peakall et al. 1995; Thorpe et al. 1994a; Waddle 1993, 1994) can consider individual variation.

This paper describes a preliminary partial Mantel test procedure for investigating the relationships between observed morphological variation and a set of factors (both ecological and historical) when there are adequate individuals, but few groups (islands). It is not proposed as a definitive procedure, but as a procedure that will give an indication of whether it is likely to be cost-effective to invest substantial effort in sampling and studying numerous populations per island, or region as in Thorpe et al. (1995).

The subject of this study, the western Canary island lacertid, *Gallotia galloti*, is a medium-sized diurnal herbivore found on Tenerife (and associated islets), La Palma, El Hierro, and La Gomera (Fig. 1). Numerous morphological characters from the scalation, color pattern, and body dimensions vary substantially among islands and within Tenerife. For example, the mature males on El Hierro tend to be small and blackish with blue spots on the legs and relatively robust heads whereas in north Tenerife they tend to be large with bright yellow dorsal cross bars, blue cheeks, and relatively gracile heads. The ecological conditions differ among islands (Garcia et al. 1990; Huetz de Lemps 1969), and molecular analyses (Thorpe et al. 1993a,b, 1994b) indicate that there is a distinct intraspecific phylogeny with northern and southern lineages. Consequently, this morphological variation could reflect the intraspecific phylogeny (Thorpe 1984; Thorpe et al. 1993a,b, 1994b) and/or natural selection for the different ecological conditions (Brown et al. 1991; Malhotra and Thorpe 1991a,b; Thorpe 1991; Thorpe and Brown 1989) among islands.

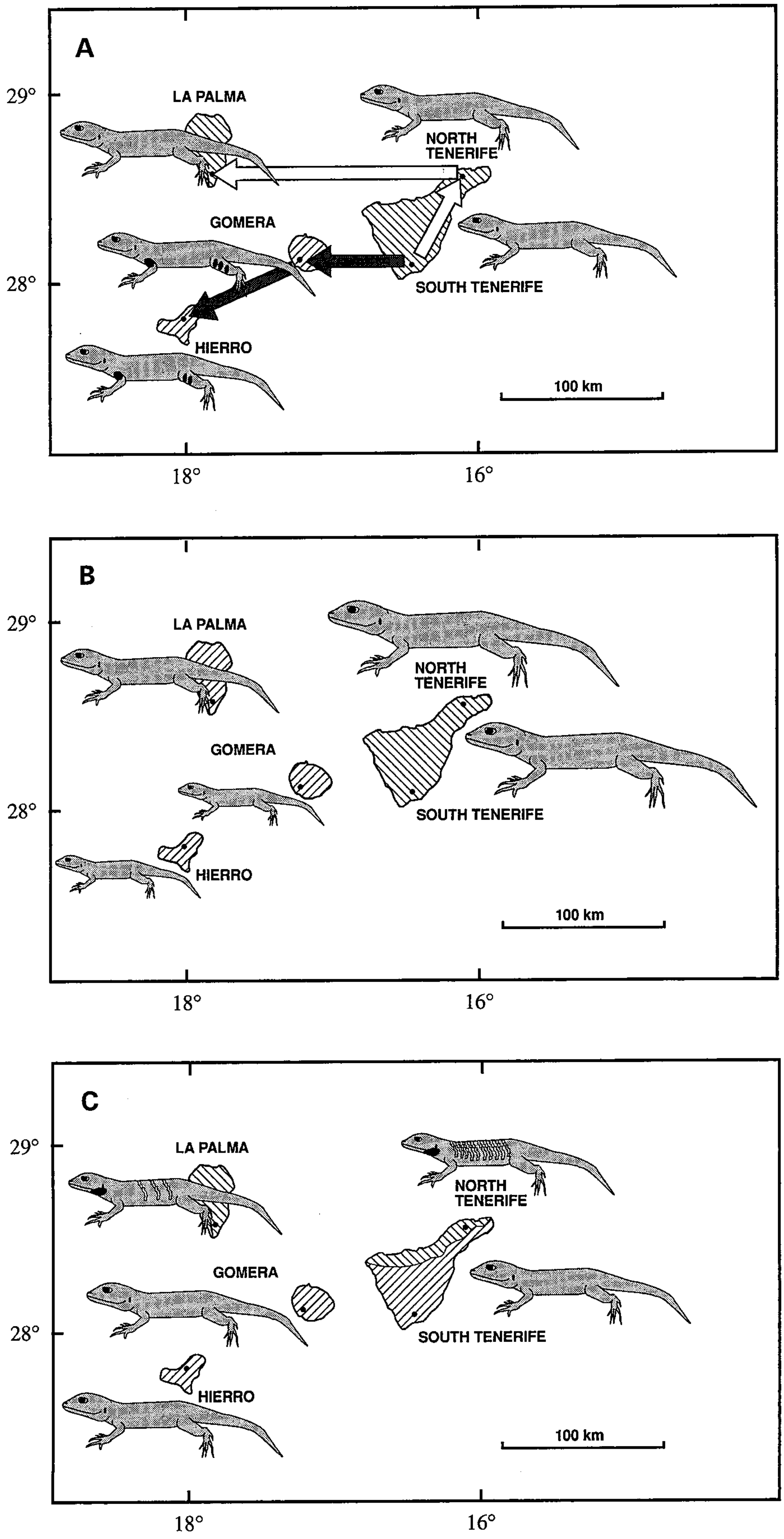
To test the extent to which the phylogeny and ecogenetic factors are correlated to the geographic variation in a given morphological character, one needs to be able to represent the phylogenetic relationships largely independent of any ecogenetic (natural selection) effects. Although one can attempt to reconstruct a phylogeny based on morphology for these populations, (Thorpe et al. 1985), it is not possible to use this to test hypotheses free of circularity as much, or even all, of the variation may be due to ecogenetic adaptation to current conditions. The least selectively influenced information that is readily available for constructing phylogenetic relationships at this level is mitochonarnal DNA (mtDNA) nucleotide sequence.

In this study relatively neutral DNA information (Miyamoto and Cracraft 1992) is used to construct phylogenetic relationships among populations, and this is used in combination with recently developed partial Mantel tests that allow several interacting hypotheses to be tested simultaneously (Manly 1991; Thorpe 1991; Brown et al. 1991; Sokal et al. 1991). This enables the relative importance of historical and ecogenetic effects to be tested. It is particularly important to be able to test as many factors as is necessary simultaneously because they can be intercorrelated. This procedure is useful in this, and other, intraspecific interisland studies where both historical factors and a range of ecological factors can play an important role in determining morphological evolution.

MATERIALS AND METHODS

Morphological features that were readily standardized and readily recordable from every appropriate individual, and which represent a range of character systems, were selected for an earlier study of the intraspecific and interspecific morphology of *Gallotia* species (Thorpe et al. 1985). For this intraspecific study, 10 body measurements, 10 scalation characters, and 10 color-pattern characters (sexually mature males) are appropriate and are presented in (Table 1). These were recorded from specimens from north Tenerife (17), south Tenerife (11), El Hierro (11), La Palma (13), and La Gomera (13). Body-dimension characters were adjusted for size independence by a pooled within-group regression against snout–vent length.

Mantel procedures can test for an association between two matrices using randomization (Manly 1986a,b). The parameter (such as a correlation or regression coefficient) is compared with the distribution obtained when the matrix is repeatedly randomized. The null hypothesis of no association is rejected when the parameter value is exceeded in the randomizations at a given probability level. The reliability of the probability depends on the number of randomizations (Jackson and Somer 1989) so in this study 10,000 are employed. The association between an observed pattern of variation between individual cases (Excoffier and Smouse 1994;


A
29°
28°
LA PALMA
NORTH TENERIFE
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SOUTH TENERIFE
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B
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LA PALMA
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SOUTH TENERIFE
HIERRO
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18°
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C
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LA PALMA
NORTH TENERIFE
GOMERA
SOUTH TENERIFE
HIERRO
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16°

TABLE 1. Partial Mantel tests. The null hypothesis probabilities for the standardized absolute partial regression for each of the three factors are given with $P < 0.0167$ (Bonferroni corrected by 0.05/3 hypotheses) and marked with an asterisk to indicate that they have reached significance according to the sequential Bonferroni correction considering all 90 probabilities (0.05/3 hypotheses × 30 characters). Characters 2 through 10 are body dimensions adjusted by pooled within-group regression for size independence, characters 11 through 20 are scalation characters, and characters 21 through 30 are color-pattern characters, which, together with character 1, are based on sexually mature males. Island codes are NT (north Tenerife), ST (south Tenerife), LP (La Palma), GM (La Gomera), and HI (El Hierro).

	Probabilities for hypotheses			Means for islands/regions				
Character	Phylog	Biodiv	Climate	NT	ST	LP	GM	HI
1 SV length	0.0018	0.0001*	—	11.5	11.3	9.8	8.6	8.3
2 Head length	—	—	0.0163	21.2	21.0	20.0	21.8	21.1
3 Head width	—	—	0.0005*	9.7	10.0	9.4	10.2	9.9
4 Prefrontal length	—	—	0.0001*	1.4	1.7	1.0	1.6	1.4
5 Frontonasal width	0.0028	0.0000*	—	3.6	3.6	3.2	3.3	3.2
6 Mouth-ear distance	0.0128	—	—	3.1	2.9	2.8	3.4	3.1
7 Eye-mouth distance	—	—	0.0001*	4.6	5.2	4.3	4.9	4.7
8 Eye-ear distance	—	—	0.0000*	5.6	6.1	5.5	6.1	5.7
9 Ear height	0.0030	0.0040	0.0014	4.2	4.7	4.0	4.3	4.3
10 Head depth	—	—	0.0000*	9.0	9.4	8.7	9.4	9.3
11 Pectoral no.	0.0005*	—	0.0144	6.6	6.1	7.4	6.4	7.6
12 TS ventral no.	0.0104	0.0003*	0.0037	12.5	13.6	11.1	11.9	10.6
13 TS dorsal no.	0.0063	—	—	94.8	85.8	92.6	89.2	96.3
14 Collar no.	—	0.0000*	—	11.7	12.2	11.6	9.7	9.2
15 Crenulated collar	0.0001*	0.0001*	—	0.1	0.4	0.5	1.0	1.0
16 Femoral pores	0.0000*	0.0135	0.0044	27.9	25.2	28.4	26.1	29.6
17 Postoc. temporal no.	0.0095	0.0003*	—	2.8	2.6	2.2	1.3	2.0
18 Labial temporal no.	—	—	0.0017	3.2	2.8	2.2	3.3	2.3
19 Frontonasal shape	—	0.0148	—	0.7	0.5	1.0	0.7	1.0
20 Single chinshield	0.0006*	0.0001*	0.0006*	1.0	0.4	0.2	0.2	0.0
21 Blue cheek	—	—	0.0000*	1.0	0.0	1.0	0.0	0.0
22 Blue massateric	—	—	0.0008*	0.3	0.0	0.5	0.0	0.0
23 Height blue cheek	—	—	0.0000*	4.2	0.0	2.3	0.0	0.0
24 Length blue cheek	—	—	0.0000*	5.8	0.0	9.0	0.0	0.0
25 Blue lateral no.	0.0000*	0.0076	0.0040	4.2	6.6	6.8	2.3	2.1
26 Light lateral no.	0.0000*	—	—	7.2	6.9	7.8	4.7	2.1
27 Blue trunk no.	0.0000*	—	0.0073	3.2	5.6	5.3	1.3	1.1
28 Blue foreleg spot no.	0.0001*	—	—	0.0	0.0	0.0	1.2	0.7
29 Blue hindleg spot no.	0.0000*	—	—	0.0	0.0	0.2	2.9	1.8
30 Yellow bar no.	0.0042	0.0045	0.0000*	10.0	0.3	3.2	0.3	0.0

Peakall et al. 1995; Thorpe et al. 1994a; Waddle 1993, 1994), or geographic sample means (Thorpe et al. 1995), or species, represented as a similarity matrix (dependent variable), and a pattern of variation derived from a given causal hypothesis, or factor, also represented as a matrix (independent variable), can be tested in this way. This procedure allows one to reject a causal hypothesis on the evidence provided. This may provide a basis for more detailed investigation into the mechanisms of causation for hypotheses that cannot be rejected. The observed pattern of variation (dependent matrix) may be very detailed, whereas a causal hypothesis may generate a simple pattern. For example, Legendre and Fortin (1989), tested the association between an environmental matrix between individual cases and a simple binary model matrix between cases. They consider this procedure to resemble a nonparametric "discriminant function."

One's ability to reject hypotheses is enhanced by considering several hypotheses simultaneously, because these hypotheses may produce intercorrelated patterns, and in fact more than one factor could be contributing to the pattern of geographic variation. Partial Mantel tests that consider numerous factors simultaneously (Manly 1991) are therefore a considerable advance over simple Mantel tests. The observed pattern of variation is treated as the dependent variable with each hypothesized pattern treated as one of several independent variables, which are considered simultaneously to produce as partial regression (or correlation).

In this study, partial Mantel tests (Manly 1991) were per-

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FIG. 1. (A) *Phylogenesis.* Schematic representation of evolution in the western Canary Island Lacertid, *Gallotia galloti.* The arrows indicate the rigorously hypothesized colonization sequence (Thorpe et al. 1994b) of the two lineages westward (northern lineage, empty arrows; southern lineage, shaded arrows). The blue spots on the foreleg (ch. 28) and hindleg (ch. 29), thought to be for conspecific sexual communication, are present in the southern lineage (Gomera and Hierro) and absent in the northern lineage (north Tenerife, south Tenerife, and La Palma) and outgroups, irrespective of ecological conditions. (B) *Ecogenesis.* Irrespective of phylogenetic lineage, sexually mature males are large in biodiverse areas (Tenerife), progressively smaller in more depauperate areas (La Palma), and smallest in the most depauperate areas (Gomera and Hierro). (C) *Ecogenesis.* Irrespective of phylogenetic lineage, wet, lush areas (north Tenerife and La Palma) have disruptive dorsal yellow bars, blue cheeks for conspecific communication, and gracile heads.

formed with the variation in each individual morphological character, represented as a taxonomic distance matrix between individuals, as the dependent variable. The patterns generated from the various ecological (biotic and physical) hypotheses and the phylogeny were considered simultaneously as independent variables. All these matrices were transformed to normalized vectors (zero mean, unit variance) before being input into the partial Mantel test so that the measure of association between the morphological character (dependent variable) and an independent variable is given as the absolute standardized partial regression. The partial Mantel program was supplied by Manly, with associated programming by Thorpe.

FACTORS

The factors under consideration that may have determined the pattern of variation are the phylogenetic relationships among populations, the biotic environment, and the physical environment. The phylogeny may determine the pattern of variation in the sense that the variation reflects the historical phylogenetic process to which the species has been subject, whereas the latter two factors may be regarded as being causative agents based on natural selection for current ecological conditions. The null hypothesis of no association between the observed pattern and each of the three factors is tabulated when the probability is less than 0.0167 (Bonferroni corrected 0.05/3) but is rejected only when the probability is less than the more demanding sequential Bonferroni correction (Rice 1989) taken across all 90 values (0.05/3 hypotheses × 30 characters).

Phylogeny.—The phylogenetic relationships used in this study are based on sequence comparisons across 1005 mtDNA base pairs (bp) (291 bp cytochrome b; 465 bp cytochrome oxidase I; 249 bp 12s ribosomal RNA [rRNA]). The materials and methods for obtaining the mtDNA sequence divergence, together with the actual 1005 bp sequence are given in Thorpe et al. (1994b). A range of phylogenetic trees, Fitch-Margoliash (without and without the assumption of a molecular clock), Wagner parsimony, and maximum likelihood, were produced from this mtDNA sequence data (Thorpe et al. 1994b). The trees were outgroup rooted by the two congeners, *G. atlantica* and *Gallotia stehlini*, as well as the mainland lacertid *Psammodromus hispanicus.* The phylogenetic relationships of the *G. galloti* populations are congruent among these trees and trees based on RFLP and RAPD nuclear DNA data (Thorpe et al. 1993a,b; Thorpe et al. 1994b). These trees show two very distinct lineages for *G. galloti*: a southern lineage (on La Gomera and El Hierro) and a northern lineage (on La Palma, north and south Tenerife). An interpretation of the phylogeny in terms of interisland colonization sequence, given in Thorpe et al. (1994b), shows two separate westward colonizations (with the DNA times being compatible in detail with island age at each stage) from older eastern islands to younger western islands (Thorpe et al. 1994b) (Fig 1A). In the north, La Palma is colonized from north Tenerife, and in the south Gomera is colonized from south Tenerife, with Hierro finally being colonized from Gomera.

Historical hypotheses, or relationships, can be expressed in a variety of ways. In this study, they could be represented by a matrix of genetic distances based on sequence similarity, by patristic distances in a phylogenetic tree, by subspecies based on lineages from molecular phylogenetic analysis (Thorpe et al. 1993b), or by the deduced colonization pathway (Thorpe et al. 1994b). Here, the patristic distances of a Fitch-Margoliash tree without the assumption of a molecular clock (Fitch and Margoliash 1967; Fitch 1971) (1005 bp sequence data), are used. This tree is presented in Thorpe et al. (1994b).

Biotic Factor: Biodiversity.—This variable attempts to express how rich or depauperate the biotic environment is. The islands differ in altitude and area and the environmental complexity and productivity they offer. Tenerife is a large, high-altitude island with high plant and animal biodiversity. In contrast, the western islands (La Palma, La Gomera, and El Hierro) tend to be smaller and depauperate with much lower biodiversity. This factor is based on Humphries' (1979) estimate of plant diversity and Baez's (1992) estimate of land-bird diversity. A taxonomic distance matrix computed across normalized plant and land-bird diversity represents this factor.

Physical Factor: Climate.—There are noticeable differences in climate and consequent vegetation (Garcia et al. 1990; Huetz de Lemps 1969) within, and among, the islands of the Canarian archipelago. Climatic differences within individual islands have been shown to influence morphological differentiation of all three types of lizards present (Thorpe et al. 1991), that is, lacertids (Thorpe 1991; Thorpe and Brown 1989; Thorpe and Baez 1987; Thorpe et al. 1994a), geckos (Thorpe 1991), and skinks (Brown and Thorpe 1991a,b; Brown et al. 1991). Northern Tenerife and La Palma tend to be wet with lush vegetation whereas south Tenerife and the sampled lowland areas of La Gomera and El Hierro tend to be arid and barren. This hypothesis is represented by a taxonomic distance matrix computed from the total annual rainfall (Heutz de Lemps 1969; Garcia et al. 1990) at, or close to, sample sites.

RESULTS AND CONCLUSIONS

In a partial Mantel test, matrices representing these three factors (independent variables) are considered simultaneously against each morphological character (dependent variable) in turn. Most characters from the three morphological character systems (adjusted body dimensions, scalation, and color pattern), show a significant relationship with one or more factors (Table 1). Body-dimension variation is most usually associated with climatic conditions, or (to a lesser extent) biodiversity; color-pattern variation is associated with the phylogeny, or climatic conditions; whereas scalation variation is associated primarily with biodiversity, or phylogeny.

Morphological variation can be associated with the phylogeny irrespective of its association with current ecological conditions. An example of morphological traits strongly associated with the phylogeny are the blue leg marks (characters 28 and 29), which are present in the southern lineage and absent in the northern lineage and all outgroups (Fig. 1A). Other characters are also clearly associated with the phylogeny; the southern lineage animals tend to have a crenulated collar fringe (character 15) and few light/blue body spots (characters 25, 26, and 27) (Table 1). Phylogeny is also associated with variation in scalation characters 11 and 20.

Irrespective of phylogeny and climate, sexually mature males tend to be smaller (character 1) on depauperate, low biodiversity, islands (Fig. 1B). Specimens from these islands also tend to have narrow frontonasals (characters 5), fewer, more frequently crenulated collar scales (characters 14 and 15), fewer temporals (characters 17) and ventrals (12), and a double chin shield (character 20) (Table 1).

Irrespective of phylogeny and biodiversity, specimens from wet lush areas (north Tenerife and La Palma) tend to have gracile heads (characters 3, 4, 7, 8, and 10) and blue cheeks (characters 21, 22, 23, and 24) and yellow dorsal bars (characters 30) (Fig. 1C). Climate also appears to be associated with scalation character 20.

When the more extreme Bonferroni correction is used most characters are associated with only a single factor, but characters 15 is associated with two factors and character 20 with all three factors.

DISCUSSION

The phylogenetic relationships of the populations obviously play an important role in determining the morphology of the island forms as 9 of the 30 morphological characters are significantly associated with the DNA phylogeny. Some characters are closely associated with the DNA phylogeny, for example, the blue leg spots. These leg spots are present only in the southern lineage, being absent in the northern lineage, both congeneric outgroups and the lacertid outgroup. Hence, they appear to be synapomorphic for the southern lineage of *G. galloti.*

The blue markings (whether on the legs, trunk or neck) are thought to have a role in conspecific signalling (Thorpe and Brown 1989). This study, and studies within individual islands (Thorpe and Brown 1989), indicate that the blue markings on the trunk and neck may be strongly influenced by ecogenesis. Studies of color-pattern variation of sexually mature males within Tenerife suggest that blue cheek/trunk markings may be for conspecific communication and yellow dorsal bars for disruptive crypsis (Thorpe and Brown 1989) in these agonistic and highly predated lizards. Thorpe and Brown's (1989) study suggested a balance between natural selection and crypsis, such that in wet, lush areas disruptive dorsal bars prevail with blue sexual marking developing on the cheek rather than trunk, whereas in south Tenerife the balance is in favor of pronounced blue marks on the trunk (Thorpe and Brown 1989). This interisland study is compatible with Thorpe and Brown's (1989) and Thorpe et al.'s (1994a) within-island study, in that the tested partial regressions do not provide evidence to reject the hypothesis that the blue cheeks and yellow dorsal bars in males are an ecogenetic adaptation to a wetter climate. Head robustness is also correlated to wet climates with lush vegetation and this may be due to ecogenetic adaptation. This may involve conspecific agonism as sexually mature males are aggressive and have larger heads than the females. Also, there may be a dietary effects on the head robustness of these vegetarian lizards as the climatic differences result in different vegetation types (Thorpe and Brown 1989).

Although body size varies greatly among species (Thorpe 1985) and substantially among island forms of the same species, it varies only slightly in correlation to climatic/altitudinal factors within single islands (Thorpe and Brown 1991; pers. obs.). It is therefore not surprising to find that it is not associated with climate although is does correlate with biodiversity. The smaller body size may be an ecogenetic adaptation to a narrower, less consistently available, food source on depauperate islands. In any event, there is no evidence of it being entirely due to direct environmental induction as specimens from different islands raised under standard laboratory conditions still show these differences in body size (pers. obs.).

Although the results of this interisland study are generally compatible with the previous series of within-island studies this is not the case with all characters. Within-island studies of lizards (Malhotra and Thorpe 1991b; Thorpe and Baez 1987; Thorpe 1991), and other studies of lizards (Horton 1972; Soule 1966; Soule and Kerfoot 1972), consistently imply that dorsal scalation is determined by ecogenetic adaptation, whereas this study does not support this interpretation for interisland variation.

Some of applications of Mantel tests at the supraspecific level have used classification to represent historical relationships (Douglas and Matthews 1992). As a rule, conventional subspecies should not be used for this purpose as detailed studies of geographic variation reveal that they generally reflect no consistently recognizable biological unit, let alone phylogenetic lineage (Thorpe 1987). Moreover, at the intraspecific level it is possible for the variation in morphological characters to be predominantly determined by adaptation for current ecological conditions and for the phylogenetic component to be minimal. Consequently, it is generally inappropriate to attempt to use a tree based on morphology in order to investigate phylogenetic and ecogenetic components of intraspecific variation in morphological characters. A tree based on independent data that has the greatest chance of selective neutrality, for example one based on mtDNA sequence, has to be preferred for this purpose.

When there are few groups it is possible to get a preliminary indication of association between characters and alternative explanatory factors by using individuals, although it may be considered to be too easy to reject the null hypothesis under these circumstances. Whether individual variation or locality means (Thorpe et al. 1995) are used, this procedure should be of general utility for investigating both ecological and phylogenetic correlates of population evolution in both morphological (e.g., size, shape, color, and scalation) and biochemical (e.g., venom) characters (Thorpe et al. 1995), and is particularly useful in areas such as interisland evolution, where it can be difficult to distinguish among various factors. If, for example, one addresses the question posed above as to why the specimens from north Tenerife and El Hierro differ in body size, color pattern and head size one can now see that the best answer currently available is that one they differ in leg markings due to phylogeny, they differ in body size in correlation with environmental depauperateness/richness, and in head robustness, cheek color and dorsal yellow markings primarily in correlation with climatic differences. The mechanism causing the latter two correlations is presumably ecogenetic adaptation.

ACKNOWLEDGMENTS

This research was funded by Natural Environment Research Council (NERC) (GR3/6943), Science and Engineering Research Council (SERC) (GR/F/19968), Carnegie and Royal Society. I would like to thank T. Garland, J. Losos, D. Bauwens, M. Baez, R. P. Brown, K. Watt, A. Malhotra, A. Cumming, D. McGregor, W. Jordan, and P. E. Smouse for assisting in various ways.

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