Molecular and morphological evolution within small islands

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5.1 Introduction

Many studies of evolution on islands, from Darwin’s (1859) time onwards, have tended to emphasize inter-island differences. However, inter-island studies (although very popular) are generally not in a position to contribute much to an understanding of relative importance of historical processes and selection on their own. There have been some efforts to distinguish between the roles of historical factors and current selection pressures (Snell et al. 1984; Gardner 1986), but they do not use the appropriate methodology to make much headway with this problem.

Some of the difficulties involved are exemplified by the inter-island differences in the endemic western Canary Island lacertid Gallotia gallopro (Fig. 5.1). The distinct differences in scaleation, colour-pattern, and body dimensions could be due to historical factors like founder effects and drift, or to adaptation to the current ecological conditions that differ among islands (Thorpe 1996). Molecular data, such as mtDNA sequence and RFLPs (which are hopefully minimally confounded by selection effects) can be used to reconstruct a phylogeny (Thorpe et al. 1994a). The western Canaries have not been joined to one another or the mainland (Carracedo 1979 and references therein). Consequently, any organism naturally distributed across them must have undergone inter-island dispersal. Given this geological background, a rigorous set of rules can be used to convert this phylogeny into a colonization sequence (Thorpe et al. 1994a; Juan et al. 1995). G. gallopro appears to have arisen on the oldest western island, and colonized the younger islands further to the west. The colonization time for each island inferred from the DNA divergence is appropriately less than the geological time of origin of each island (Thorpe et al. 1994a).

Once a quantifiable perspective of the historical relationships (with minimal selection effects) is obtained, one can test for adaptation taking into account these historical relationships using partial regression based matrix correspondence tests (see below). Historical relationships may be represented in a variety of ways, including as a matrix of patristic distances among taxa along the branches of a molecular phylogeny (Thorpe 1996; Thorpe et al. 1995, 1996; but see also Douglas and Matthews 1992). When there are only a few islands, as in the western Canaries, and each island is generally
Molecular and morphological techniques and large-scale field experiments on natural

5.2 Matrix correspondence

Tests of a null hypothesis of no association between variation and a pattern generated by
they enable hypotheses to be rejected, and patterns and hypotheses can convey a matrix of dissimilarities between
being the probability of the null hypothesis, but the probability of the null hypothesis, a matrix are not independent and
ments, which cannot be exhaustive matrices (Manly 1986a, b, 1991), if
oriation can be found. Where these variations may be intercorrelated. To these
extensions of the test are used (Sokal and Sneath 1979). Hypotheses are taken as the index

Although inter-island studies will remain popular and important, there are in-
progressive contributions of current natural selection and historical factors. More
the relative contribution of some entities to the heterogeneous entities that they are, and investigating population differen-
tial among several local populations (Thorpe and Brown 1989; Brown et al. 1991;
Malhotra and Thorpe 1991a; Castellano et al. 1994; Prentice et al. 1995; Thorpe et al.
Small islands may offer distinct advantages for these studies of microgeographic
varied, with the tendency to natural selection may vary substantially over very short geographic distances, which gives considerable logistic
advantages over mainland systems where considerable distances may be involved. The
general trend is to have a depauperate fauna with few species, which may mean that
individual species are found in densities far greater than in mainland systems. This
facilitates sampling and may allow exhaustive coverage of the species range over all
habitat types.

This chapter surveys our studies of within-island microgeographic variation that use
lizards as model organisms. This work has primarily been carried out in the Canarian
and Lesser Antillean archipelagos and can be considered under three rubrics: (1) matrix
correlation tests for association between observed patterns and patterns generated by

Geographic variation of the colour pattern of sexually ripe males

The variation in six colour patterns was studied by multivariate analysis (Thorpe 1991; 1994b) used partial regression on
the association of the pattern component matrix of 67 localities, against several hypothesized factors, such as
precursor islands, (ii) a cloud layer, (iii) elevational or ecological populations from low-altitude populations, (iv)
to latitudinal climatic/vegetational
changes, (v) geographic proximity represents obvious

vegetational biotopes can be related to
mature males may be a balance.
putative causal factors; (2) investigations of parallel patterns of variation; and (3) large-scale field experiments on natural selection.

5.2 Matrix correspondence (mantel) tests and molecular studies

Tests of a null hypothesis of no association between an observed pattern of geographic variation and a pattern generated from one or more causal hypotheses are useful in that they enable hypotheses to be rejected. When dealing with geographic patterns, both patterns and hypotheses can conveniently (and in some cases must) be represented as a matrix of dissimilarities between entities (e.g. local demes). The correspondence between the matrices can be measured by a statistic such as a correlation or regression, but the probability of the null hypotheses cannot be tabulated because the elements of a matrix are not independent and the degrees of freedom are unknown. With large matrices, which cannot be exhaustively permuted, the rows and columns of one of the matrices (Manly 1986a, b, 1991) can be randomized and the statistic recomputed. This is repeated a large number of times (e.g. 10,000 fold in Thorpe et al. (1996)) to give a distribution of the statistic so that the probability of the null hypothesis of no association can be found. Where there are several hypotheses, the patterns generated by them may be intercorrelated. To overcome this, partial correlation, or partial regression extensions of the test are used (Smouse et al. 1986) where the observed pattern, (e.g. in morphology) is taken as the dependent variable and patterns generated from the hypotheses are taken as the independent variables (Manly 1986b; Thorpe and Baez 1993).

These tests are making an important contribution to studies at the intraspecific level and have recently had a high profile (Brown et al. 1991; Sokal et al. 1991; Waddle 1994; Daltry et al. 1996; see also a review by Smouse and Long 1992). Two examples of their application to within-island geographic variation are given here; Tenerife lacertids and Dominican anoles.

Geographic variation of the lacertid G. galloti within Tenerife

The colour pattern of sexually mature male lacertids varies markedly across Tenerife. The variation in six colour pattern characters can be treated individually or combined by multivariate analysis (Thorpe and Brown 1989; Thorpe et al. 1994b). Thorpe et al. (1994b) used partial regression matrix correspondence (PRMC) methods to test the association of the pattern of geographic variation in the colour pattern, across 67 localities, against several hypotheses including (i) historical separation of ancient precursor islands, (ii) a cloud layer around Teide inducing separation of high-altitude populations from low-altitude populations, (iii) adaptation to altitude, (iv) adaptation to two latitudinal climatic/vegetational biotopes which meet along a sharp ecotone and (vi) geographic proximity representing the opportunity for gene flow and unspecified geographical components. All hypotheses except for adaptation to the climatic/vegetational biotopes can be rejected. It appears that the colour pattern of sexually mature males may be a balance between crypsis to avoid predation (overhead avian
predators see the dorsum with its disruptive yellow bars in the north) and sexual selection for lateral, blue, display markings (for laterally positioned conspecifics).

Later studies of the molecular affinities of these Tenerife populations (across largely the same set of localities) by Thorpe et al. (1996), using cytochrome b sequence data, revealed three main haplotypes which, when subjected to an outgroup rooted phylogenetic analysis, revealed eastern and western lineages. Historical relationships, whether derived from molecular or other data (Sokal et al. 1991; Waddle 1994), can also be tested against alternative historical scenarios. In this case the historical relationships are represented by the molecular phylogenetic affinities (patristic distances among populations on the molecular phylogenetic tree). These were treated as the observed (dependent) pattern. Several alternative historical hypotheses can be tested. These hypotheses are primarily based on the concept of populations existing on the ancient precursor islands that formed Tenerife (Ancochea et al. 1990). Patterns generated from these hypotheses are represented as independent variables in a PRMC test. A set of three similar patterns represented hypotheses involving a single western precursor and an eastern precursor, a fourth pattern represented separate north-western and south-western precursors, a fifth pattern represented three separate precursors, one on each of the three ancient areas, a sixth pattern representing cloud induced vicariance, with a seventh matrix representing geographic proximity. A series of pairwise matrix correspondence tests followed by a PRMC tests allows one to reject all hypotheses other than that the pattern was formed by expansion from an ancient western and an ancient eastern precursor island (Thorpe et al. 1996).

The earlier colour pattern studies made no allowance for different molecular phylogenetic lineages being present on the island. When this is allowed for by (1) testing colour pattern against biotope and geographic proximity within the eastern and western lineage separately, and (2) testing colour pattern against climatic biotopes, geographic proximity, and phylogenetic patristic distances in a PRMC test (see Thorpe et al. 1996; but also Thorpe et al. 1995; Daltry et al. 1996; Thorpe 1996) then there is still an association between colour pattern of sexually mature males and biotope.

The eastern and western lineages revealed in the mtDNA appear to have introgressed completely as there is no indication of reproductive isolation between these east–west lineages in previous quantitative morphological studies of scapulation, shape (Thorpe and Baez 1987), size (Thorpe and Brown 1991), or colour (Thorpe and Brown 1989). Indeed, natural selection of the colour pattern for current biotopes appears to have largely eradicated historical effects. The molecular lineages have an east–west pattern while colour pattern has a marked north–south pattern irrespective of lineage (Fig. 5.2). DNA times (which are compatible with geological times (Thorpe et al. 1996)) suggest this introgression occurred after about 700 000 years separation.

**Dominican anole, Anolis oculatus**

*Anolis oculatus* is the only anoline lizard on Dominica, a young volcanic island in the Lesser Antillean island chain fringing the eastern Caribbean. Dominica possesses a diverse set of climatic and vegetational regimes with littoral woodland on the Atlantic coast, xeric woodland on the Caribbean coast, and montane rain forest and cloud forest in the extremely mountainous central island and showed pronounced genetic (body shape, scapulation, and colour) structure among samples of females using an mtDNA and morphological characters (Thorpe et al. 1994a; Fig. 5.2) with the overall effects of rainfall, temperature, and vegetation type (Thorpe et al. 1994b; Malhotra and Thorpe 1995). When individual characters are tested independently, morphological data alone do not explain the variation, but with some exceptions. For example, the cyan element of body hues is reduced or absent in Dominica as shown in the molecular and morphological analyses (Thorpe in preparation; see also Th
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Fig. 5.2 Colour pattern variation and DNA lineages of Gallotia galloti on Tenerife. The line indicates the transition between northern and southern colour morphs (Thorpe and Brown 1989) which is associated with an ecotone between different climatic/vegetational biotopes. The shaded band indicates the distribution of the western and north-eastern mtDNA lineages, bearing in mind that some populations contain different haplotypes (Thorpe et al. 1996).

in the extremely mountainous centre. Anoles were sampled from 33 localities across the island and showed pronounced geographic variation in the 47 morphological characters (body shape, sculation, and colour pattern) studied (Fig. 5.3). The ‘overall’ similarity among samples of females using 47 morphological characters is strongly associated (P < 0.0001) with the overall ecological similarity among localities (using altitude, rainfall, temperature, and vegetation (Malhotra and Thorpe 1991a)) when tested with a partial matrix correspondence test which also includes geographic proximity.

A more detailed picture can be obtained by using PRMC tests to test multivariate character sets such as body shape, sculation, and colour pattern (as dependent variables) against a series of independent variables, i.e. geographic proximity, altitude, temperature, rainfall, and vegetation type. This shows that, using locality means, general body shape and colour are related to vegetation, and general sculation is related to rainfall (Thorpe et al. 1994b; Malhotra and Thorpe 1997a, b; Malhotra and Thorpe unpublished data). When individual characters are tested they generally conform to the multivariate sets, but with some exceptions. For example, relative size of enlarged lateral scales is associated with vegetation type, not rainfall (Malhotra and Thorpe 1997a), while the cyan element of body hues is related to rainfall, not vegetation type (Malhotra and Thorpe in preparation; see also Thorpe et al. 1994b).
Generally there is rather limited congruence among characters and the extent of morphological differences. However, the extent of congruence among characters is marked while the ecological difference is 22% variability across the 33 lineages. A 50% consensus tree was constructed using both parsimony and cladistic results. Because of the high variability across the 33 lineages, it was clear, and revealed the presence of a phylogenetic tree supported (appearing in 100% of 100 bootstrap replications at a rate of 2.5% Ma⁻¹). Populations belonging to the Caribbean coast (Fig. 5.4b) overlap with the transition between north and south Caribbean lineages, but also have a degree of overlap with the phylogenetic relationships defined at the transition between north and south Caribbean lineages. The map shows no relationship to the position of lava flows. The morphological and ecological data are incompatible.

Moreover, when a phylogenetic tree was added to partial morphological (47 characters of 50) and morphological (47 characters of 50) morphological characters, the inclusion and exclusion of phylogenetic characters closely associated with phylogeny, i.e., colour pattern and body proportions (Bonferroni correction against the pertinent ecological factor), suggests a Bonferroni correction (Bonferroni correction).
Generally there is rather limited congruence in geographic variation in individual characters and the extent of morphological difference is commensurate with the extent of ecological difference. However, along the Caribbean coast the morphological change is marked while the ecological change is subtle. Moreover, there is a higher degree of congruence among characters in this area. This raises the question as to whether there is a phylogenetic/historical component to this geographic variation along the Caribbean coast.

A 267bp section of the mtDNA cytochrome b gene was sequenced which showed 22% variability across the 33 localities. A phylogenetic tree (Fig. 5.4) was reconstructed using both parsimony and distance-based methods, which gave very similar results. Because of the high variability, there were many equally parsimonious reconstructions, but a 50% consensus tree was resolved to a surprisingly high degree (Fig. 5.4a), and revealed the presence of several lineages. The most basal split is the best supported (appearing in 100% of all trees) and would have occurred 4 Ma ago (using a rate of 2.5% Ma^{-1}). Populations belonging to this lineage are found in the central part of the Caribbean coast (Fig 5.4b) and the southern edge of its range may be close to the transition between north and south Caribbean ecotypes. Other lineages are more closely related, but also have a degree of geographical coherence when mapped. Nevertheless, the phylogenetic relationships do not adequately explain the morphological difference between north and south Caribbean coast populations. The geographical distribution of lineages shows no relationship to current or known past barriers to gene flow (i.e. position of lava flows). The most divergent populations in terms of mitochondrial sequence are completely introgressed morphologically with populations further north. Although the morphologically differentiated southern Caribbean coast populations do belong to a single lineage, it appears to be relatively recently derived, and its only peculiar feature is that it has a lower haplotype diversity compared with other lineages, but this may simply be a consequence of the somewhat lower population densities in this part of the island.

Moreover, when a 'phylogenetic' distance matrix derived from this sequence information was added to partial matrix correspondence tests comparing generalized morphological (47 characters of females) with generalized ecology and geographic proximity, then morphology remains associated with ecology ($P < 0.0001$ with both the inclusion and exclusion of phylogeny), whereas generalized morphology is not closely associated with phylogeny ($P = 0.0168$), or proximity ($P = 0.2385$). The null hypotheses of no association has to be accepted for the last two variables after Bonferroni correction across the three independent variables (0.05/3 = 0.0167). Each character system is associated with an aspect of the ecology. This association is not changed when a partial matrix correspondence test is used to test each system in turn against the pertinent ecological factor together with geographic proximity and DNA phylogeny, i.e. colour pattern and body proportions are still associated with vegetation ($P < 0.0001$, $P < 0.0011$ respectively), and scolation is associated with rainfall ($P < 0.0001$). These tests show no association between the DNA phylogeny and scolation ($P = 0.72$), or body proportions ($P = 0.72$), although there is a significant (but slight) association between DNA phylogeny and colour pattern ($P = 0.0151$) even after Bonferroni correction.
Consequently, the population understanding of the morphological differences could be natural selection for current ecological conditions.

### 5.3 Parallels

Several species on the same islands show similar latitudinal and longitudes and the ground lizard, *Ameiva fasciata*, (Malhotra and Thorpe 1991), the gecko, *Tarentola delallandi* (Thorpe et al. 1993) show similar latitudinal and longitudes, a longitudinal pattern of variation. Similar, the gecko, *C. sextineatus* (Brown and Thorpe 1993), the gecko, *Tarentola delallandi* (Thorpe et al. 1993), show similar latitudinal and longitudes, a longitudinal pattern of variation.

These similar patterns within and between islands within a region are typical of many species and within a region. This is because organisms in similar environments are not independent. It is likely that species with similar adaptations have undergone similar evolutionary processes. Therefore, it is likely that similar adaptations have evolved under similar environmental conditions. This is because organisms in similar environments are likely to have similar adaptations. Therefore, it is likely that similar evolutionary processes have occurred in similar environments. Therefore, it is likely that similar evolutionary processes have occurred in similar environments.
Consequently, the population phylogeny may contribute something to the understanding of the morphological differentiation, but the overwhelming factor appears to be natural selection for current ecological conditions.

5.3 Parallels


These similar patterns within a single island are, on their own, of limited utility in differentiating between historical vicariance and selection for current ecological conditions. This is because organisms on a common island may have been subject to both the same historical/geological processes at a given time, and the same ecological differentiation. However, when there are islands within archipelagos which have independent histories but common ecological zonation, then parallel patterns of geographic variation and directions of character state change, among different species on different islands, argue for natural selection for adaptation to this zonation because it is the ecological zonation they have in common, not their internal history. Two examples have been elucidated using lizards, the Canary Island skinks and the Lesser Antillean anoles.

**Canary Island skinks**

The high-elevation islands of Tenerife and Gran Canaria, in the Canarian archipelago, both receive wind-borne rain predominantly from the north. This results in similar ecological zonation in both islands, with a lush, warm, humid habitat on the north-facing slopes (below the 1500 m inversion level in Tenerife) and a barren, hot, arid habitat in the south. The skink, *C. sexlineatus*, shows very pronounced geographic variation across 47 localities within Gran Canaria, in its scalation (Brown and Thorpe 1991a), body shape and size (Brown and Thorpe 1991a), and colour pattern (Brown and Thorpe 1991b). Similarly, the skink, *C. viridanus*, shows geographic variation across 17 localities within Tenerife (Brown et al. 1993). The colour pattern variation is particularly noticeable, and in both islands the pattern of geographic variation is shown only to be associated with these climatic biotopes when PRMC tests are employed (Brown et al. 1991). In both islands, skinks (both males and females) from the north have brown tails, while those in the south have bright blue tails. Tail autotomy is known to be an antipredator mechanism in lizards, which may be more effective when the tail
is conspicuously coloured (Cooper and Vitt 1986). This parallel change in character state, in concert with parallel change in ecological conditions on two independent islands, provides support for the role of natural selection in adapting tail colour for different antipredator strategies in the different habitat types.

Lesser Antillean anoles

The central Lesser Antilles are a series of high-altitude islands with parallel ecological zonation that offers opportunities to investigate parallel patterns in their endemic anoles. Parallel patterns in the morphology of Anolis oculatus on Dominica and Anolis marmoratus on the neighbouring island of Basse Terre (Guadeloupe) were investigated. Basse Terre belongs to the same period of orogenesis as Dominica and is very similar in topography, climate, and vegetation. In essence, it is a mirror image of Dominica, as the highest mountain is in the south of Basse Terre, but in the north of Dominica. Thus the rain shadow effect results in the south-west coast of Basse Terre and the north-west coast of Dominica being the driest regions of the respective islands. As well as being closely related, these anoles are ecologically similar. Both are solitary species which are widely distributed in a number of different habitats and show a wide range of morphological variation.

The 17 morphological characters (colour pattern, scelation, and body dimensions) recorded were selected from an analysis of morphological variation in A. oculatus on the basis of high-between-locality F-ratios and large squared multiple correlations with ecological variables. Finally, characters showing clear homologies with A. oculatus were favoured. This was particularly relevant for colour pattern characters. Males from 25 localities in Basse Terre were investigated and morphological distance matrices representing multivariate generalizations of the three character systems were derived. These dependent variable matrices were each compared with several independent variable matrices representing environmental variation (as described above) using a PRMC test.

The relationship between morphology and environmental variation found in A. marmoratus was similar to those found in A. oculatus. In both species, generalized scelation is correlated with rainfall, and generalized colour pattern with vegetation type ($P < 0.0005$). There are also parallel state changes in individual characters; body size is significantly correlated with both altitude and rainfall, the number of body scales is significantly correlated with rainfall and altitude, and the number of spots with the occurrence of dry scrub woodland (Malhotra and Thorpe 1994).

The parallel variation strongly suggests that natural selection is responsible for determining morphological geographic variation in these anoles. It may also give us some insight into the cause of differentiation of southern Caribbean coast populations of A. oculatus in Dominica, as a corresponding parallel cline is observed on the Caribbean coast of Basse Terre (Malhotra and Thorpe 1994). This suggests a non-historical cause common to both species, and raises the possibility that an ecological factor that is important to the lizard, but is not obvious to humans, does vary along the Caribbean coast of both islands. An intriguing twist to this parallel variation is added by the parallel variation in cytochrome b sequence of these two species along the

Caribbean coast (Malhotra and Thorpe 1994). This suggests some morphological and ecological convergence in the conventional interpretation of mitochondrial DNA data for selecting effects. However, the cytochrome b variation across both species is very low.

Other islands in the Lesser Antilles also show parallel variation. A series of islands with similar patterns, and having a single evolutionary history and orographic history may be less extreme (e.g. Montserrat). Nevertheless, populations on Montserrat indicate that there are some differences. For example, male Anolis luciae (St. Martin) show variation in generalized colour pattern, and some of Anolis lividus (Montserrat) populations. This species also shows a parallel and significant change in males ($P < 0.00009$).

5.4 Field experiments on Anolis oculatus

Relatively few rigorously tested experiments on natural populations exist (Endler 1986; Price et al. 1984; Price et al. 1984). None of these islands provide such a demonstration of parallel variation in A. oculatus.

Anolis oculatus, while being a relatively short generation time, has a high degree of phenotypic variation. It studies the four ecological zones the extent of relative ecological difference is great. Caribbean coast habitats are very diverse, intermediate between the former and latter.

In this experiment, large-scale field trials in different habitats. Four enclosures were placed in xeric woodland on the northern populations (representing the former habitat). One enclosure contained a transplanted population from the Atlantic (east) coast of the Caribbean. The transplanted population from the tropical rainforest experiment. Before marking and tagging morphological characters (Malhotra and Thorpe 1994).
Consequently, the population phylogeny may contribute something to the understanding of the morphological differentiation, but the overwhelming factor appears to be natural selection for current ecological conditions.

5.3 Parallels

Several species on the same island may show similar patterns of geographic variation. For example in Tenerife the lacertid, G. galloii (Thorpe and Brown 1989, 1991), the gecko, Tarentola delallandi (Thorpe 1991), and the skink, Chalcides viridanus (Brown et al. 1993) show similar latitudinal patterns. In Dominica the anole, Anolis oculatus (Malhotra and Thorpe 1991), the iguana, Iguana delicatissima (Day unpublished data), and the ground lizard, Ameiva fasciata (Malhotra and Thorpe 1995) show, to varying degrees, a longitudinal pattern of geographic variation with differences between the Caribbean and Atlantic coasts. Similarly, on Gran Canaria the lacertid, G. stehlini (Thorpe and Boaz 1993), the gecko, Tarentola boettgeri (Thorpe unpublished data) and the skink, C. sexlineatus (Brown and Thorpe 1991a, b) all show a latitudinal pattern of geographic variation.

These similar patterns within a single island are, on their own, of limited utility in differentiating between historical vicariance and selection for current ecological conditions. This is because organisms on a common island may have been subject to both the same historical/geological processes at a given time, and the same ecological differentiation. However, when there are islands within archipelagos which have independent histories but common ecological zonation, then parallel patterns of geographic variation and directions of character state change, among different species on different islands, argue for natural selection for adaptation to this zonation because it is the ecological zonation they have in common, not their internal history. Two examples have been elucidated using lizards, the Canary Island skinks and the Lesser Antillean anoles.

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Caribbean coast (Malhotra and Thorpe 1994). The sequence variation is congruent with some morphological and ecological clines. At first sight this conflicts with the conventional interpretation of mtDNA variation as reflecting historical changes rather than selection effects. However, a fuller understanding will require a detailed study of cytochrome b variation across both islands.

Other islands in the Lesser Antilles present the opportunity for further tests of parallel variation. A series of islands of independent origin, sharing the same climatic patterns, and having a single endemic species of anole, are present. However, the orogenic history is more complex for some (e.g. St Lucia, Martinique) and the contrast between habitat types may be less pronounced for smaller, less mountainous islands (e.g. Montserrat). Nevertheless, preliminary results from studies in progress on these islands indicate that there are some parallels in common across all these species. For example, male Anolis luciae (St Lucia) show a parallel association between patterns of variation in generalized colour pattern and vegetation (P < 0.0100) as do both sexes of Anolis lividus (Montserrat) (P < 0.0052 males, P < 0.0004 females). The latter species also shows a parallel association between scalation and moisture levels in females (P < 0.0090).

5.4 Field experiments on selection

Relatively few rigorously tested, direct demonstrations of current selection in natural populations exist (Endler 1986; but see Endler 1980; Halikka and Raatikainen 1975; Knights 1979; Price et al. 1984). The aim of this manipulative field experiment was to provide such a demonstration of the action of natural selection on morphological variation in A. oculatus.

Anolis oculatus, while being a relatively k-selected anole (Andrews 1979), has a relatively short generation time, with juveniles reaching sexual maturity in under a year. Other features of its population structure that make it especially suitable for such a study are its extremely high population density, territorial behaviour, and striking degree of phenotypic variation. Since the geographic variation in morphology relates to the four ecological zones the extremes of the continuum are referred to as ecotypes. The relative ecological difference between the habitats indicates the north and south Caribbean coast habitats are very similar, and the Atlantic coast habitat is somewhat intermediate between the former and that of the montane habitat.

In this experiment, large-scale lizard-proof enclosures were constructed in two different habitats. Four enclosures were constructed (Malhotra and Thorpe 1993) in xeric woodland on the northern Caribbean (west) coast, and samples of four source populations (representing the four ecotypes) were translocated into these enclosures. One enclosure contained a ‘resident’ control, which was subjected to the same procedures as translocated ‘foreign’ ecotypes. Similarly, two enclosures were constructed on the Atlantic (east) coast containing one resident control population and one translocated population from the Caribbean coast, thus providing a partial reciprocal experiment. Before marking and releasing into the appropriate enclosure, 10 morphological characters (Malhotra and Thorpe 1991b) were recorded from each lizard (which was...
individually marked by toe clipping). This multivariate phenotypic profile was later used to compare morphology of survivors and non-survivors (lizards were not re-measured). The west-coast enclosures (1 to 4) were stocked in June/July 1990 (at the start of the wet season) and monitored in September 1990. The two east-coast enclosures (5 and 6) were stocked in September 1990 and monitored in February 1991.

Multivariate morphological differences between survivors and non-survivors were tested. As the morphological differences between sexes and between ecotypes also needed to be taken into account, a three-way multivariate analysis of variance (MANOVA) was used initially for the west-coast experiment. The model included interactions between sex (male or female), survival (survivor or non-survivor), and ecotype (north Caribbean, south Caribbean, montane, Atlantic). The interaction between survival and ecotype reveals whether the magnitude of morphological difference between survivors and non-survivors is greater in some enclosures than others. A canonical variate analysis was then performed on all groups for each experiment (4 ecotypes × 2 sexes × survival/non-survival = 16 groups for the west-coast experiment and 8 groups for the east-coast experiment). Since the ecotypes differ considerably in size, a possible bias may be introduced into the analysis. Although canonical analysis takes into account the intercorrelating effects of size, this was checked by size-adjusting the linear measurements prior to the analysis, and repeating this with SVL included and excluded. In all cases, the results were unaltered (Thorpe and Malhotra 1992).

**West-coast experiment**

The results of a three-way MANOVA show a highly significant interaction exists between enclosure and survival versus non-survival ($P < 0.001$). This implies the existence of varying selection intensity between the ecotypes. The multivariate distance (Mahalanobis $D^2$) between the morphology of survivors and non-survivors of each ecotype was obtained from the canonical analysis. After only two months, the montane population was already showing significant differences between morphology of survivors and non-survivors ($P < 0.01$ for males and $P < 0.001$ for females) (Malhotra and Thorpe 1991b).

In order to examine the relationship between selection intensity (represented by the extent of morphological separation between survivors and non-survivors of each ecotype) and the extent of ecological change experienced by the translocated populations more rigorously, the ecological dissimilarity was plotted against the morphological dissimilarity ($D^2$) averaged across the sexes (see also Malhotra and Thorpe 1991b). A curve of best fit to the four data points gave a correlation of 1.0, which is significant ($P < 0.01$) even with the one degree of freedom left by adopting this curvilinear model (Thorpe and Malhotra 1992). This suggests that the intensity of selection on the different population was strongly dependent on the magnitude of ecological change experienced.

**East-coast experiment**

Few animals in the transferred population survived until the first monitoring session. Even so, in males, there is a significant difference between the morphology of survivors and non-survivors of the translocated lizards, but not in the control littoral zone (Thorpe and Malhotra 1992).

There is much discussion of these results in terms of evolutionary processes (Phylogenetic methods) and the potential for these changes to occur on a short time scale within single generations, strongly for the differences among the ecotypes at the current ecological conditions. Finding here a significant difference in morphological急忙 translocated ecotypes but no difference between survivors and non-survivors of the enclosure habitat and the habitat.

**5.5 Conclusions**

Although explicit rules can be developed from a molecular phylogeny, total partitioning historical factors fail to predict all demographic changes that limit efficacy where there are no significant changes. Studying the genetic diversity of populations over time provides a better understanding of the factors affecting population differentiation.

This overview reveals that evolutionary processes are not always simple, as morphological differentiation may be influenced by a variety of factors. A more complete understanding of the factors affecting population differentiation may be achieved through the study of ecological interactions and the interplay between genetic and ecological processes. The role that these interactions play in the maintenance of genetic diversity and the potential for adaptation to changing environmental conditions remains an important area for future research.
5.6 Summary

The sequence of inter-island colonization events can be hypothesized from a molecular phylogeny with the aid of explicit rules. Statistical methods can be used to assist in partitioning historical factors from current selective factors, but they are of limited efficacy when the number of islands is small. Studying numerous populations within small, but heterogeneous, islands allows a better understanding of the factors causing geographic variation. Three main approaches have been used to study within-island geographic variation in lizards on Canarian and Lesser Antillean archipelagos: (1) matrix correspondence tests and their partial regression/correlation extensions on morphological and molecular data; (2) identification of within-island patterns of morphological geographic variation in parallel on independent islands; and (3) large-scale field experiments on selection. These studies reveal that, even on small islands, 'island populations' may not be homogeneous in morphology, or molecular phylogeny, and that adaptation to current ecological conditions appears to be a primary force influencing morphological population differentiation, irrespective of phylogenetic history.

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### 6 Speciation

**Peter R. Grant**

#### 6.1 Introduction

The biology of islands is the biology of speciation. How does speciation occur? This is a complex question. Studies of species have been divided into two broad categories: those that occur naturally on islands and those that are introduced. The former are known as island species and the latter as mainland species.

Studies of organisms on islands have shown that evolutionary processes are often different from those occurring on the mainland. For example, in island species, speciation can occur more rapidly than on the mainland due to the isolation of a population from the mainland. This isolation can lead to the development of new species that are adapted to the local environment.

In this chapter, we will review the current understanding of speciation on islands and discuss some of the key factors that influence the process. We will also discuss the role of evolutionary processes such as genetic drift, gene flow, and natural selection in the formation of new species.

Some of the key components of speciation on islands include genetic drift, gene flow, natural selection, and genetic isolation. Genetic drift is the random fluctuations in allele frequencies due to chance. Gene flow is the transfer of genetic material between populations. Natural selection is the differential survival and reproduction of individuals due to their genetic makeup. Genetic isolation is the separation of populations from each other, which can lead to the development of new species.

The process of speciation is often complex and involves multiple factors. For example, speciation can occur through a process known as adaptive radiation, in which a single species splits into multiple species that are adapted to different habitats.

In conclusion, the biology of islands is the biology of speciation. The study of island species provides a unique opportunity to understand the processes that drive the evolution of new species. Understanding these processes is crucial for conservation efforts and for our understanding of the diversity of life on Earth.

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6.1 Introduction: A brief overview of the biology of islands and the process of speciation. Speciation occurs through a combination of genetic drift, gene flow, natural selection, and genetic isolation. For example, in island species, speciation can occur more rapidly than on the mainland due to the isolation of a population from the mainland.