

Adaptive differentiation following experimental island colonization in *Anolis* lizards

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If colonizing populations are displaced into an environment that is often very different from that of their source¹, they are particularly likely to diverge evolutionarily, the more so because they are usually small and thus likely to change by genetic restructuring or drift^{2,3}. Despite its fundamental importance, the consequence of colonization for traits of founding popula-

tions have primarily been surmised from static present-day distributions^{1,2,4,5}, laboratory experiments⁶ and the outcomes of haphazard human introductions⁷⁻⁹, rather than from replicated field experiments. Here we report long-term results of just such an experimental study. Populations of the lizard *Anolis sagrei*, introduced onto small islands from a nearby source, differentiated from each other rapidly over a 10-14-year period. The more different the recipient island's vegetation from that of the source, the greater the magnitude of differentiation. Further, the direction of differentiation followed an expectation based on the evolutionary diversification of insular *Anolis* over its entire geographic range. In addition to providing a glimpse of adaptive dynamics in one of the most extensive generic radiations on earth, the results lend support to the general argument that environment determines the evolution of morphology.

Propagules of 5 or 10 lizards (2:3 male:female ratio) were introduced onto 14 small islands near Staniel Cay, Exumas, Bahamas, in 1977 (11 islands)¹⁰ and 1981 (3 islands). Lizards were collected from Staniel Cay and randomly assigned to islands that did not contain lizards naturally (probably because of periodic hurricanes). On all but some of the smaller islands, lizard populations have persisted and, on some islands, thrived; one island attained a population of over 700 lizards. Consequently, these introductions constitute a replicated experiment of the effect of island characteristics and founder propagule size on differentiation among colonizing populations. The source of the introductions, Staniel Cay (roughly 3 × 1 km), is covered by a variety of vegetation including substantial amounts of coppice, a scrubby to moderately tall forest formation¹¹. Staniel contrasts markedly with the experimental islands, which have few trees and are mostly covered by narrow-diameter vegetation.

The extensive research on the evolutionary radiation of *Anolis* lizards in the Caribbean provides the framework within which these experiments were conducted. On the basis of macroevolutionary and among-population studies of *Anolis* adaptation to structural habitat, we can formulate *a priori* predictions about how introduced populations should adapt to the new structural habitats on the experimental islands. Comparisons among and within species of *Anolis* indicate that hindlimb length evolves in response to changes in the mean diameter of perches, producing a positive correlation between limb length and utilized perch diameter¹²; functional studies indicate that this correlation is probably the result of a trade-off between maximal locomotor abilities increasing with limb length versus the ability to move efficiently on narrow surfaces decreasing with limb length¹³. These macroevolutionary patterns are sufficient to make the following predictions about how anoles adapt to changes in vegetational structure: (1) the degree to which experimental populations diverge morphologically from the source population should correlate with the degree to which the vegetation structure on an experimental island differs from that on Staniel Cay; and (2) among populations, a positive relationship should exist between relative hindlimb length and mean perch diameter.

In May 1991, adult male lizards were captured and morphological measurements taken on most of the experimental islands still having lizards. In addition, 41 male *A. sagrei* were captured from the areas on Staniel Cay that the lizards for the original introductions came from. We removed the effects of size from morphological variables (see Methods) to examine differences in shape of lizards from each of the experimental islands and Staniel Cay. Populations differed in shape (Table 1, columns 3 and 4, bottom), but not body size (Table 1, column 1). Figure 1a plots the position of the populations on Staniel Cay and the experimental islands in a morphological space defined by the first two shape axes (that is, from principal components analysis on size-adjusted variables). Although the Staniel individuals were randomly distributed about their population centroid (the mean value for the two axes), with no uni- or bimodal pattern (Rayleigh's test of circular distribution,

$z = 0.70$, $P > 0.50$), the experimental islands have clearly differentiated non-randomly with respect to the source population ($z = 7.12$, $P < 0.001$); most of the experimental island centroids lie in a 90° sector relative to the Staniel centroid. The position of experimental island centroids in this two-dimensional morphological space indicates that lizards on the experimental islands had relatively shorter limbs, and, to a lesser extent, wider toe-pads and greater mass than the lizards from Staniel Cay (Fig. 1b).

Both of our hypotheses about how morphology should diverge in relation to habitat structure were confirmed. First, a relationship existed between how different the vegetation on an experimental island was from the source island and how much the population on that experimental island diverged morphologically from the source

population ($r = 0.55$, $P < 0.025$, one-tailed, Fig. 2). Analysis of covariance with vegetational difference as the covariate gave no significant effect of propagule size ($P > 0.25$). Second, a positive relationship also existed between size-adjusted hindlimb length and perch diameter used (including Staniel: $r = 0.59$, $P < 0.025$, Fig. 3; not including Staniel: $r = 0.58$, $P < 0.025$; both comparisons one-tailed).

Although rates of evolution as rapid as observed in this study are not uncommon in introduced populations¹⁴, rarely has the adaptive nature of this change been so clear-cut. In this case, the extensive knowledge of *Anolis* natural history and evolution allows *a priori* prediction of patterns of differentiation among populations introduced to an environment markedly different from the environment

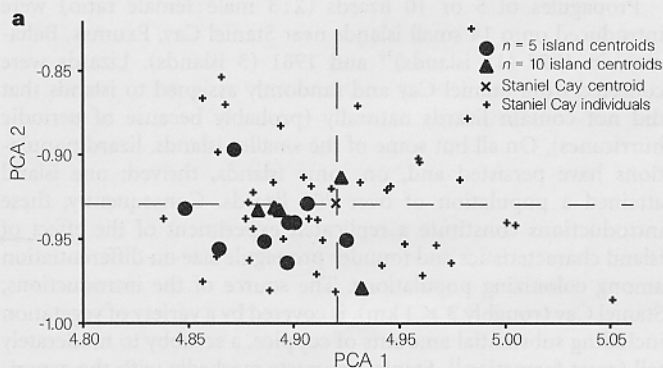


Table 1 Differentiation in size and shape among experimental populations

| Variables | Pooled within-island analysis | | Size-adjusted analysis | |
|-------------------|-------------------------------|--------------------|------------------------|--------|
| | Axis 1* | Shape coefficient† | Axis 1 | Axis 2 |
| Snout-vent length | 0.92 | 0.83 | 0.55 | -0.11 |
| Forelimb length | 0.80 | 0.64 | 0.81 | 0.43 |
| Hindlimb length | 0.77 | 0.60 | 0.86 | 0.38 |
| Lamellae width | 0.94 | 1.56 | -0.96 | 0.29 |
| Mass | 0.90 | 1.05 | 0.33 | -0.92 |
| Variance (%) | 80.9 | | 59.9 | 26.5 |
| With Staniel‡ | | | | |
| | $F = 0.549$ | | 2.757 | 2.754 |
| | $P = 0.88$ | | 0.002 | 0.002 |
| Without Staniel‡ | | | | |
| | $F = 0.632$ | | 2.398 | 3.967 |
| | $P = 0.80$ | | 0.01 | 0.0001 |

Size accounted for 81% of the pooled within-island variance. The loadings were large and positive for all dimensions, which indicates that the correlation between each dimension and size was large (first column).

* Size (see text).

† Multivariate allometric coefficients for the slope of the regression line relating each variable to the first principal component.

‡ Results of analysis of variance.

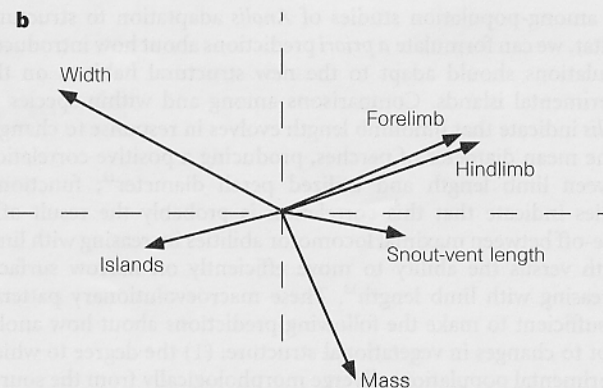


Figure 1 a, Morphological space defined by the first two size-adjusted principal components axes (PCA). Circles are the centroids for islands founded with propagules of five individuals, triangles are the centroids for islands founded with propagules of 10 individuals, the x is the centroid for the source population (Staniel), and pluses (+) are individuals from Staniel. Rate of evolution was calculated separately for the two principal component axes and ranged from 0–955 darwins for axis 1 and 0–2,117 darwins for axis 2. **b**, All vectors, except 'islands', indicate the direction and loading of each variable, ln-transformed, on the two principal components axes from the size-adjusted analyses. For example, hindlimb length loads strongly and positively on PC1 and weakly and positively on PC 2. These vectors indicate, for example, that most populations have moved in the opposite direction from the limb vectors, indicating shorter limbs. The vector labelled 'islands' marks the direction of the mean angle for the centroids of the experimental islands. This is a directional vector only (that is, length of the vector is arbitrary).

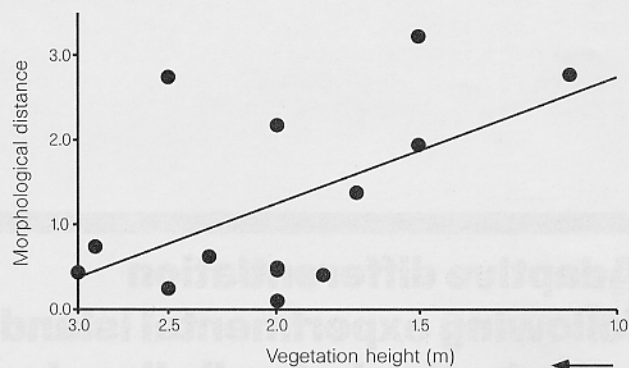


Figure 2 Vegetation height of experimental islands versus the morphological (Mahalanobis) distance of the population on that island from the Staniel population. The scale of the x-axis (from large to small heights) is reversed to emphasize that islands with low vegetation are more dissimilar from Staniel than are islands with high vegetation. Maximum vegetation height on each island was used as a measure of vegetational differences among islands; on similarly sized islands near Georgetown, Bahamas, which is less than 100 km from our study site, maximum height is related to a variety of measures of vegetation structure, such as mean vegetation height ($r = 0.82$, $P < 0.0005$, $n = 14$) and mean vegetation diameter at a height of 12 ($r = 0.53$, $P < 0.05$, $n = 14$) and 36 inches ($r = 0.62$, $P < 0.025$, $n = 12$ (two islands had too little vegetation tall enough to measure at 36 inches); all comparisons one-tailed; J.B.L. and D. Spiller, unpublished results). Staniel Cay, the source island, has vegetation considerably broader and higher than on any of the experimental islands, with some trees greater than 10 m tall. Differences in vegetation height among islands may also correlate with other variables affecting these lizards, such as available thermal microclimates.

of the source island. Further, the substantial replication of these introductions allows an examination of the concordance between the degree to which the new environment is different from the source environment and the extent to which experimental populations have differentiated. Taken together, these results indicate that founding populations of *A. sagrei*, despite their small initial size, can survive and rapidly adapt to the new environmental conditions in their new habitat.

An important parallel exists between patterns of adaptive differentiation reported here for one species of *Anolis* and patterns apparent among species of *Anolis* in the entire Caribbean *Anolis* radiation, which has produced nearly 150 species (250 more occur in Central and South America). In both cases, differences in limb dimensions are related to differences in microhabitat structure, although the differences are considerably greater among Greater Antillean species^{12,15}. This study thus indicates that not only can populations rapidly respond to new environmental conditions, but also that the response is in some ways qualitatively similar to large-scale patterns manifest on macroevolutionary timescales. This suggests that the processes operating during adaptive radiation may be similar to those producing microevolutionary adaptation—macroevolution may just be microevolution writ large—and, consequently, that insight into the former may result from study of the latter.

However, another mechanism could also produce divergence among our experimental populations similar to that seen in macroevolutionary time. In recent years, awareness of the adaptive importance of non-genetic environmental effects on morphological size and shape of animals has grown (for example refs 16, 17). A variety of environmental differences among experimental islands could potentially lead to morphological differences. The most plausible of these is differences in the diameter of vegetation used by the lizards. The different bone stresses produced by living on surfaces of different diameters could plausibly cause the limbs of lizards to grow at different rates. However, most studies (for example, refs 18, 19) of the effect of physical exertion on limb growth (all on endotherms) generally have noted differences in bone density or diameter, rather than in length, although there have been some exceptions (such as ref. 20). If this developmental hypothesis is correct, then the evolution of the large morphological differences that characterize the *Anolis* adaptive radiation may be the outcome of selection operating on a trait with an initially large environmental component. This would indicate that phenotypic plasticity may have macroevolutionary significance, as proposed in a hypothesis formulated nearly 50 years ago^{21–24}. Further observation and experimentation will be necessary to determine whether this is the case or whether the purely evolutionary hypothesis is correct. □

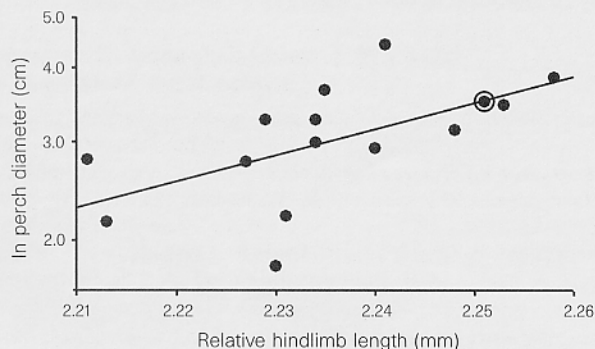


Figure 3 Relationship between mean perch diameter (ln-transformed) used and size-adjusted hindlimb length in populations of the lizard *Anolis sagrei* on islands near Staniel Cay, Bahamas. Circled point indicates Staniel. The rate of evolution of size adjusted hindlimb length varied from 89–1,195 darwins.

Methods

Data collection. The following measurements were taken on each lizard (sample size on the experimental islands = 1–14; \bar{x} = 8.6): snout-vent length (svl), mass, fore- and hindlimb length, and width of the subdigital pad on the fourth hindtoe (lamella width). No individuals from the source population were measured or preserved at the time of the introductions because the experiment was designed to test very different hypotheses from those examined here¹⁰. Habitat use by the lizards was measured by recording the height and perch diameter for each male lizard observed (sample size = 7–57; \bar{x} = 26.7). The range in vegetated area occupied by lizards for experimental islands was 89–5,790 m². Although island species turnover is much lower for lizards than many other kinds of organisms²⁵, it does occur. Thus, dispersal between naturally occupied and experimental populations is possible; its precise importance remains to be determined by future theoretical and empirical evaluation.

Multivariate analysis of size differentiation. We define size as the first principal component from a pooled within-island matrix of morphological variables, thus following rubric 2 in ref. 26. The pooled within-group matrix is equal to the error mean square matrix from a MANOVA^{27,28}. We justified the use of this multivariate size dimension, rather than a univariate size dimension, because each of the five morphological variables increases at different rates with lizard growth, and only the adjusted mass dimension approached isometry (Table 1, column 2). Because variance-covariance matrices require that all variables be measured in the same units, we converted mass to a linear dimension using the equation²⁹ adjusted mass (mm) = 35 × mass^{0.34}. Thus, no one dimension best represents size because each dimension represents growth in a different way. Therefore, a multivariate size dimension that (1) uses information from all univariate dimensions, (2) accounts for the variance-covariance structure of the data set and (3) quantifies allometry, best characterizes growth or ontogenetic size (other methods (such as ref. 12) produce qualitatively similar results).

Multivariate shape analyses. We removed the effects of size from the original log-transformed data set using the method of Burnaby³⁰. A principal components analysis using a total variance-covariance matrix was then conducted on these size-adjusted variables. This produced composite shape variables based on the covariance structure of a size-free data set. To quantify the extent to which the populations diverged from the source population, we calculated the Mahalanobis distance in morphometric space, defined by the first two size-adjusted principal component axes, from each experimental population to the Staniel population. Populations on islands 13 and 25¹⁰ could not be included in the Burnaby analysis because of their small sample sizes; for these populations, size-adjusted variables were calculated by projecting the ln-transformed variables from each captured lizard from these two islands onto the original Burnaby size-adjusted plane defined using the other islands. Mahalanobis distances were estimated for the populations on these two islands using the pooled variance-covariance structure of the other islands.

Rates of evolution. Rates of morphological evolution were calculated as $r = (\ln(x_2) - \ln(x_1))/\Delta t$, where r = rate of change (in darwins), x_1 and x_2 are the initial and final dimensions of the character, and Δt is the time elapsed in millions of years. These rates were compared to those calculated for a variety of other recently introduced species¹⁴.

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