Adaptive differentiation following experimental island colonization in *Anolis* lizards

Jonathan B. Losos†, Kenneth I. Warheit†
& Thomas W. Schoener‡

†Department of Biology, Campus Box 1137, Washington University, St Louis, Missouri 63130-4899, USA
‡Department of Fish and Wildlife, 600 Capitol Way North, Olympia, Washington 98501-1091 and Burke Museum, DB-10, University of Washington, Seattle, Washington 98195, USA

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

1. Download the full text of the article [here](https://www.nature.com/articles/387701a0).
In the title,
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 species13,15. 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 macroevolutionary 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 ago11,24. 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 (in-transformed) and size-adjusted hindlimb length in populations of the lizard Anolis sagrei on islands near Stoneloe Cay, Bahamas. Circled point indicates Stoneloe. The rate of evolution of size-adjusted hindlimb length varied from 8.0–11.6 cm/darwin.

Methods

Data collection. The following measurements were taken on each lizard (sample size on the experimental islands = 1–14; z = 8.61; 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 here. Habitat use by the lizards was measured by recording the height and perch diameter for each male lizard observed (sample size = 7–57; x = 26.7). The range in vegetated area occupied by lizards for experimental islands was 89.5790 m². Although island species turnover is much lower for lizards than many other kinds of organisms2, 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 ref. 16 in ref. 26. The pooled within-group matrix is equal to the original mean square matrix from a MANOVA2,27. 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 equation26 adjusted mass (mm) = 35 × mass m. 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 analysis. We removed the effects of size from the original log-transformed data set using the method of Burnaby26. 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 25 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 in-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 ρ = (ln(x2) − ln(x1))/Δt, where ρ = rate of change (in darwins), x1 and x2 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 species26.

Received 27 November 1996; accepted 3 March 1997.


Acknowledgements. We thank M. Krutowski, R. Lewis, S. Binning, S. Rohwer, J. Smith, D. Spiller, S. Sultin, S. Schwartz and the 1993 Bicic Museum discussion group for helpful assistance and suggestions and the NSF for support. We also thank the Bahamian government for permission to do this work.

Correspondence and requests for materials to J.B.L. (Louis@biocdc.wust.edu).