

Systematics and micro-evolution

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Introduction

Darwin's theory of evolution by natural selection is the central theory of modern biology. It has been greatly modified and extended, for example by the facts of genetics and the concept of genetic drift. Nevertheless current evolutionary theory is recognizably Darwinian. Contrast this with systematics, a field of biology to which evolutionary theory applies. Systematics, the study of relationships among organisms, has been more than modified, it has been truly transformed, and the transformation has occurred relatively recently. For the first three quarters of the past hundred years systematists established relationships among taxa by using phenotypic data to assess similarities. With the advent of electrophoresis in 1966 (Hubby & Lewontin 1966), and subsequent development of biochemical and molecular techniques like DNA-DNA hybridization, DNA fingerprinting, and gene amplification and sequencing, systematics has become increasingly grounded in genetics. The second element in the recent revolution has been the development of cladistic principles (and others) to be used in the reconstruction of phylogenies. An avian systematist of the 1890s, allowed a return visit in the 1990s, would be delighted to see that a classification of all 9672 bird species of the world has been accomplished (Sibley & Ahlquist 1990, Sibley & Monroe 1990), would be pleased to recognize familiar taxonomic categories like species, genera and orders, but would be bewildered by the way in which we assign particular birds to them.

Our returning Victorian would be similarly amazed at how the modern Elizabethan uses systematic information to gain an understanding of evolution. Having identified systematic relationships among taxa we would like to know the processes that gave rise to them, by what routes, why, where and how quickly. This is a field of inferential investigation of past evolutionary processes. It is pursued in various ways. The search for fossils is the obvious, but often limited, way. Mathematical modelling can help by showing what could have occurred and what could not have occurred, given plausible assumptions. Investigation is also popularly pursued by studies of contemporary processes; by the study of behaviour, ecology and micro-evolution of existing populations, which are the products of those past evolutionary processes.

In this article I will describe how a study of micro-evolution as a contemporary, observable, process has been used to throw light on evolution in the past.

Micro-evolution

Evolution is organic change, change that takes place from one generation to another in the genetic constitution of a population. Small changes accumulating over long periods of time give rise to large differences, such

as those between 2 species in different but related genera or families. Micro-evolution refers to the small individual changes.

I make a distinction between the genetic changes taking place from one generation to the next, micro-evolution, and the evolutionary forces such as natural selection acting within a generation that produce an evolutionary effect. Natural selection occurs when some individuals in a population survive or reproduce better than others because they possess traits that enable them to perform better in that particular environment. If there is a heritable basis to those traits then the genes governing them will be passed on to the next generation. Differential gene transmission to the next generation is micro-evolution. Evolutionary processes other than natural selection may also give rise to or contribute to micro-evolution: sexual selection, mutation, immigration and drift.

I next make a distinction between selection inferred and selection observed.

Natural selection and adaptation

Differences between related taxa are in need of explanation. For example, birds on islands are often larger, and have larger beaks, than their relatives (same or different species) in nearby continental regions (Murphy 1938, Grant 1965). If islands have been colonized by birds from the mainland, as is likely to be generally the case, and evolution has been greater in the island population than in the mainland population since the time of colonization, the traits of the island birds need to be explained. Adaptation is suggested when the traits can be associated with some feature of the island, for example when beak size can be correlated with food size (Grant 1965, 1966, 1968, 1979a,b). The role of natural selection has been inferred.

The functional significance of variation in external traits like beak size is relatively easy to assess (Bowman 1961), and this facilitates investigation of adaptation (Arnold 1983). The task is much more difficult with internal anatomical features. Absence of association between trait expression and environmental characteristic suggests that evolution has proceeded by random processes like founder effects and drift. Models of the expected rate of divergence under drift can be employed to make quantitative tests of the drift (or selection) hypothesis (e.g. Baker *et al.* 1990).

Natural selection as a contemporary process

The direct study of natural selection requires something very different. It requires following the fates of known individuals through time to see if success or failure in survival and reproduction (fitness) is associated or not with the possession of a trait or the particular expression of a trait. An early example is the demonstration in 1974 of non-random survival in 2 populations of Darwin's Finches on the Galápagos island of Daphne Major. Surviving Medium Ground Finches *Geospiza fortis* had longer bill tips than non-survivors, and surviving Cactus Finches *G. scandens* varied less in weight and beak depth than non-survivors (Grant *et al.* 1976). The first is an example of directional selection, the second an example of stabilizing selection.

Since then there have been several studies of natural selection in bird populations, carried out mainly in the last dozen years and for different purposes. Price & Boag (1987) summarized the first ones, and discussed methods of analysis (see also Endler 1986). More recent studies have included selection on plumage variation (Møller 1989, Grant 1990, Hill 1991), on various morphological attributes including beak size and body size variation (Grant & Grant 1989a,b, Smith 1990, Hakkarainen & Korpimäki 1991, Witzell 1991) and on migratory tendency (Berthold 1991).

While quantitative, observational, studies such as these are needed to document, describe, and measure natural selection, they can do no more than suggest the causes of selection. Experiments are required to test selection hypotheses that specify causes.

Heritable variation

The direct study of micro-evolution requires that there be heritable variation. The methods of quantitative genetics have been applied to many of the same populations that have been investigated for evidence of natural selection. Boag & van Noordwijk (1987) provide a thorough review of methods, problems and accomplishments. A general finding has been that morphological traits such as beak size and body size have high heritabilities, whereas life history traits such as clutch size have lower but not negligible heritabilities. There is heritable variation in migratory tendency (Berthold 1991) and plumage traits (Møller 1989, Grant 1990, Hill 1991). Indeed the absence of significant heritable variation for well investigated traits (e.g. Gibbs 1988) is the exception rather than the rule, at least according to published studies.

DARWIN'S FINCHES

Micro-evolution of Darwin's Finches has been studied on Isla Daphne Major. The island is small (0.34 km^2), close to the equator in the centre of the Galápagos archipelago, and 8 km from the nearest large islands of Santa Cruz and Baltra. Two species have resident populations; *Geospiza fortis* (Medium Ground Finch) and *G. scandens* (Cactus Finch). Two others occasionally immigrate and rarely stay to breed: *G. fuliginosa* (Small Ground Finch) and *G. magnirostris* (Large Ground Finch). Birds have been ringed and measured since 1973. Breeding has been studied in every year when it has occurred between 1976 and 1991, almost all nests have been found, nestlings ringed and the parents identified by observation. Harmonic mean breeding population sizes were 197 *G. fortis*, 94 *G. scandens*, 6 *G. fuliginosa* and 4 *G. magnirostris* (Grant & Grant 1992).

Natural selection

Three episodes of natural selection have been witnessed (Table 1) at times of high mortality. The first and strongest occurred from late 1976 to the end of 1977. Almost no rain fell between March 1976 and January 1978. Of the 640 ringed *G. fortis* alive at the beginning of this period only 97 (15%) survived to the end. Mortality was size-selective; large birds survived better than small birds. *G. scandens* experienced a similar size-selective mortality, although less intensely. Survival was 42%.

TABLE I

Heritabilities and coefficients of selection for 4 morphological traits of *Geospiza fortis* on Isla Daphne Major. Selection coefficients are standardized selection differentials. Sample sizes refer to pairs of parents followed by numbers of offspring in the heritability column, and numbers of measured birds alive before selection occurred in the other columns. ¹ = not significantly different from zero ($P > 0.05$).

	Heritability h^2	Selection coefficients		
		1976–1977	1981–1982	1984–85
Weight	0.91	0.62	0.15	–0.18
Bill length	0.65	0.49	0.13	–0.09 ¹
Bill depth	0.79	0.60	0.12	–0.18
Bill width	0.90	0.49	0.08 ¹	–0.21
Sample sizes	39, 82	640	197	496
Mortality	—	0.85	0.35	0.64

Dry conditions occurred again in 1981–1982, and *G. fortis* was subjected to the same directional selection, though to a smaller degree than in 1977. Survival was much higher (65 %) this time.

The final episode occurred in the aftermath of an extremely severe El Niño event in 1982–83, which brought an extraordinary amount of rain to the Galápagos and resulted in some finches breeding for as many as 8 times. Breeding occurred twice in 1984, and then not again until 1987, another El Niño year, except for attempts made by some individuals in 1986. During the dry period without breeding from mid-1984 to the end of 1985 *G. fortis* were subjected to natural selection in the opposite direction; small birds survived better than large birds. From 1987 onwards mortality has been random with respect to size.

The targets of natural selection

When forces of selection act on one trait, other traits which are correlated with it are affected. Phenotypic correlations among the measured morphological traits are all positive and moderately large in the 3 populations of Darwin's Finches that have been studied in detail: *G. fortis* and *G. scandens* on Daphne (Boag 1983) and *G. conirostris* on I. Genovesa (Grant 1983). Thus when natural selection occurs, all traits shift in the same direction, although to different degrees, and it is not possible to determine by inspection of coefficients of overall selection like those in Table 1 whether selection acts on one or a suite of traits.

The problem of identifying the targets of selection is solved by using Lande & Arnold's (1983) multiple regression method which separates the direct association between fitness and a trait from the indirect ones, arising from correlations among traits (see also Crespi 1990). Price *et al.* (1984a) applied this method to the Daphne data from 1976–77 and found that the 4 traits listed in Table 1 were selected in different directions: weight and beak depth to increase and beak width to decrease. Beak length was not selected at all. Beak width was selected to decrease in 1984–85 as well (Gibbs & Grant 1987).

Identifying the targets helps in the interpretation of selection. Boag & Grant (1981) hypothesized that large birds survived the drought of 1977

relatively well in part because, possessing deep beaks, they were able to crack the large and hard seeds that remained in moderate abundance after the initially large stock of small seeds had been depleted. The analysis of targets supports the hypothesis, but reveals other targets not explained by it. Similarly Gibbs & Grant (1987) could account for selection in the opposite direction in terms of an altered composition of the food supply.

Heritable variation

Beak and body size traits display high levels of heritable variation. Boag (1983) regressed measurements of fully grown *G. fortis* offspring on mid-parent values to obtain the estimates shown in Table 1. All are significantly different from zero. Heritabilities of other measured traits, wing and tarsus length, are similarly high.

Micro-evolution

With such high heritabilities and strong coefficients of selection, evolution is expected to occur. The product of the heritability of a trait and the selection coefficient gives the simplest prediction of an evolutionary response to selection (Falconer 1989). More complicated formulations take into account the correlations among traits (Lande 1979, Price & Boag 1987). These will be discussed below. Boag (1983) used the first component from a principal components analysis of all morphological measurements to characterize overall body size, calculated the heritability of this synthetic trait (0.75) and the selection coefficient during the 1976–77 episode, and predicted an evolutionary response to selection of 0.40 standard deviations. The actual response in this trait—the difference between the population average before selection and the average in the next generation born in 1978—was 0.36 standard deviations, and hence close to the predicted amount. Therefore micro-evolution had occurred, as predicted: average body size was larger in the next generation as a result of a small scale evolutionary change.

Evolution occurred in the opposite direction in 1984–85. The generation born in 1987, like their parents, were smaller on average than the population in 1984 before selection had occurred.

The magnitude of selection and evolution can be most simply expressed as a percentage change in the mean of a population. For example, the selection episode of 1976–77 resulted in an increase in mean beak depth of about 5%. Evolutionary change was a little more than three quarters of this, c. 4%. Selection in the opposite direction in 1984–85 resulted in a shift in the mean of 2–3% and an evolutionary change in the same range.

Changes accompanying speciation

Clusters of Darwin's Finches differ from each other in size and shape, but not in plumage colour and pattern (Lack 1947, Grant 1986). The systematic relationships among them are not well established. Nevertheless biochemical similarities (Yang & Patton 1981) closely parallel morphological similarities (Schluter 1984), and agree in defining as one cluster the 6 species commonly known as ground finches (genus *Geospiza*). Within this

group, what phenotypic and genetic changes took place during speciation and subsequently, and can modern studies of natural selection help us to understand these transformations?

First, comparisons of phenotypic data show the magnitude of the changes involved. Thus if ancestral *G. fortis* gave rise to *G. magnirostris*, without themselves undergoing any further change, then the difference between modern *G. fortis* and *G. magnirostris* represents the minimum change involved in speciation plus some fraction that occurred afterwards. These differences are relatively small. All coexisting species of ground finches differ in at least one beak dimension by at least 15% so another way of posing the same question is to ask how much selection is required to produce a shift of this size.

Secondly, genetic data show how much evolution can be expected from selection of a given magnitude. The heritabilities of all *G. fortis* traits are all high, so evolutionary changes should not fall far below those caused by selection. Heritabilities for *G. scandens* traits on Daphne are generally lower, and those for *G. conirostris* traits on Genovesa are intermediate (Grant 1983). Heritabilities for beak depth are 0.79 for *G. fortis* (Boag 1983), 0.80 for *G. scandens* (Price *et al.* 1984b) and 0.69 for *G. conirostris* (Grant 1983).

Thirdly, measurements of natural selection provide an estimate of how much change can be expected in single steps. The largest values obtained, in the study on Daphne are 5% for selection and 4% for evolution.

Putting these 3 quantities together yields the number of episodes of strongest observed selection that are sufficient to transform the beak depth of one species into that of another. The answer is 4. That is, 4 episodes of selection each resulting in an evolutionary change of 4% would result in a net change of 15%.

Speciation and multivariate evolution

Species are more than one dimension. The multidimensional equivalent to the preceding exercise requires an equation that incorporates several characters and their correlations. Lande's (1979) equation of multivariate evolution does this. A vector of phenotypic differences between 2 populations or species in several dimensions is equated to the product, as before, of heritability and selection; but now heritability is a matrix of genetic variances and covariances, and selection is a vector of the direct effects of selection on each of the characters independent of the correlated effects.

For the ground finches, the genetic matrix is known for one species, *G. fortis*, as are the several phenotypic differences between species, and they can be used to calculate minimal forces of selection in terms of a vector length. Vector lengths are found to be small when species differ principally in size, such as *G. fortis* compared with either *G. fuliginosa* (2.28) and *G. magnirostris* (2.76), and large when species differ in proportions, as is the case with *G. fortis* and *G. scandens* (15.39).

The vector length associated with the morphological changes in *G. fortis* brought about by the drought of 1977 was 0.12. Under selection regimes of this sort, approximately 20 such episodes would be required to transform *G. fortis* into *G. magnirostris*, a much larger number than was

calculated by considering beak depth alone. Inclusion of other characters in the analysis is likely to increase that number. Nevertheless if one such episode occurred each century, the transformation of a population of *G. fortis* into *G. magnirostris* would take the comparatively short time of 2000 years. In contrast, the transformation from *G. fortis* to *G. scandens* would take about 13,000 years.

Conclusions

Measurements of the properties and performance of contemporary populations can be used to reconstruct past evolutionary processes. A knowledge of current selection regimes and heritable variation in Darwin's finch populations enables us to estimate the amount of selection that could account for differences between species. The principal results are that transitions between species differing largely in size could have proceeded rapidly, and more rapidly than for those differing in proportions owing to the constraining influence of genetic correlations between morphological traits. In reaching these conclusions I have ignored several complications (see Price *et al.* 1984b, Grant 1986, Boag & van Noordwijk 1987, Price & Boag 1987, Schluter 1989). These render questionable the accuracy of the calculations but not the overall result that selective forces are powerful enough to result in speciation relatively quickly. Sexual selection (Price 1984, Lande & Kirkpatrick 1988) and drift (Grant & Grant 1992) could have been contributing influences.

Discussion

The task of trying to understand the evolution of a particular group of organisms like passerine birds is made difficult by the incompleteness of the group. Many species, perhaps the vast majority, have become extinct, and it is unlikely that we will ever know much about them. Another difficulty arises from the fact that species may occupy geographical ranges far removed from their sites of origin. For example, British bird species probably did not evolve, as species, in Britain. Missing species and missing environments make evolutionary systematics a science that works with partial information.

Set against these difficulties are the successes which have been achieved in this and related disciplines. No class of organisms of comparable size is as well known systematically or biogeographically as birds. While animals like *Drosophila* are much better known genetically, the combined knowledge of ecology, behaviour, distribution, systematics and genetics of birds is without equal.

What can we expect in the future, and in particular from the study of micro-evolution? With the human genome project underway we can look forward to a time in the next century when some bird species will be completely characterized genetically. It is technically feasible to determine the complete architecture of avian genomes in individuals, and with this information to quantify precisely the variation among individuals within populations, between populations and between species; and it is feasible to determine the rates and sites at which new variants arise by mutation.

Expanding data banks of genetic information will permit advances to be made in 3 areas of relevance to this essay. First, they will permit refinements of systematic knowledge and the reconstruction of phylogeny. They will show in quantitative terms just how much genetic change is involved in speciation as well as in the evolution of higher taxa, and where in the genome those changes occur. Secondly, they will permit a deeper understanding of development, and of the interplay between the genome and its environment which occurs during development; in other words, a knowledge of genetic structure will facilitate the study of function. This information will be essential for understanding the genetic and developmental constraints on, and potentialities of, evolution (e.g. see Schluter 1989). The diversity of passerine birds has been produced by evolution subject to guiding rules which are scarcely understood. We do not know how malleable, genetically, species are, and in what ways.

Thirdly, they will deepen our knowledge of the genetic consequences of natural selection, and make more precise our understanding of the micro-evolutionary processes I have described in this paper. Eventually we may look forward to a detailed understanding of beak size and body size variation in genetic and environmental terms; to a knowledge of the number of genes involved, and to the sites, timing, mode and magnitude of their action. One of the reasons why micro-evolution of birds has not been studied more is the difficulty of capturing the adult offspring of known parents for heritability determination. Nevertheless there already exists an under-exploited potential to compare genetic characteristics of adults and young by molecular analysis of DNA extracted from blood samples from nestlings and parents. The potential will expand as genetic data banks expand, and intergenerational comparisons will be made in selected populations to determine the interplay of selection, drift and other evolutionary forces in bringing about evolutionary change.

Darwin's Finches have provided a good starting point for using micro-evolution to interpret larger evolutionary transformations that happened in the past. There is both need and opportunity to increase the scope of such studies. The traits investigated so far are entirely morphometric, which is appropriate because it is these that distinguish closely-related members of the ground finch group of species. But many species differ in plumage traits and only trivially if at all in morphometric traits. Plumage traits are important functionally as well as systematically. They may evolve under sexual selection and function in species recognition. Models of genetic variation and measurements of selection will provide the means of extrapolating from micro- to macro-evolution.

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