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SELECTED ABSTRACTS

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Grant, P. R., and Grant, B. R. (1997). Genetics and the origin of bird species. *Proceedings of the National Academy of Sciences USA.* **94**: 7768-7775.

External (environmental) factors affecting the speciation of birds are better known than the internal (genetic) factors. The opposite is true for several groups of invertebrates, Drosophila being the outstanding example. Ideas about the genetics of speciation in general trace back to Dobzhansky who worked with Drosophila. These ideas are an insufficient guide for reconstructing speciation in birds for two main reasons. First, speciation in birds proceeds with the evolution of behavioral barriers to interbreeding; postmating isolation usually evolves much later, perhaps after gene exchange has all but ceased. As a consequence of the slow evolution of postmating isolating factors the scope for reinforcement of premating isolation is small, whereas the opportunity for introgressive hybridization to influence the evolution of diverging species is large. Second, premating isolation may arise from nongenetic, cultural causes; isolation may be affected partly by song, a trait that is culturally inherited through an imprinting-like process in many, but not all, groups of birds. Thus the genetic basis to the origin of bird species is to be sought in the inheritance of adult traits that are subject to natural and sexual selection. Some of the factors involved in premating isolation (plumage, morphology, and behavior) are under single-gene control, most are under polygenic control. The genetic basis of the origin of postmating isolating factors affecting the early development of embryos (viability) and reproductive physiology (sterility) is almost completely unknown. Bird speciation is facilitated by small population size, involves few genetic changes, and occurs relatively rapidly.

Grant, P. R., and Grant, B. R. (1997). Hybridization, sexual imprinting, and mate choice. *American Naturalist* **149:** 1-28.

Hybridization of animal species is a special pattern of mating and hence a behavioral phenomenon, influenced by ecological, demographic, and individual factors. We examine demographic factors (sex ratio and mate availability) and characteristics of individuals (song and morphology) in an attempt to understand the occasional hybridization of three species of Darwin's finches (genus Geospiza) on the small Galapagos island of Daphne Major. We use field data from a 20-yr study to test five hypotheses. A relative scarcity of conspecific mates (the Hubbs principle) explains the hybridization of the rarer species (Geospiza fuliginosa and Geospiza scandens) but not the common species (Geospiza fortis). Female G. fortis pair with male Geospiza fuliginosa that sing songs similar to their own fathers' songs. Morphological trait values of their G. fuliginosa mates were also correlated with the trait values of their fathers. Geospiza fortis females pair with G. scandens that are morphologically similar to their mothers. These results imply that heterospecific mate choice is influenced by auditory and visual imprinting on parental traits in early life, consistent with the findings of laboratory studies of other groups of finches. Hybridization is most likely to occur when imprinting syndromes of closely related species are similar.

Grant, B. R., and Grant, P. R. (1996). Cultural inheritance of song and its role in the evolution of Darwin's Finches. *Evolution* **50**: 2471-2487.

Songs of Darwin's finches were studied on the Galapagos Island of Daphne Major from 1976 to 1995. A single, structurally simple, and unvarying song is sung throughout life by each male of the two common species, Geospiza fortis (medium ground finch) and G. scandens (cactus finch). Songs of the two species differ strongly in quantitative features, and individual variation among males is much broader in G. fortis than in G. scandens. Although there are exceptions, songs of sons strongly resemble the songs of their fathers. They also resemble the songs of their paternal grandfathers, but not their maternal grandfathers, indicating that they are culturally inherited and not genetically inherited. Female G. fortis display a tendency to avoid mating with males that sing the same type of song as their father. They also avoid mating with males that sing heterospecific song, with very rare exceptions. Thus song, an evolving, culturally inherited trait, is an important factor in species recognition and mate choice. It constrains the mating of females to conspecifics, even when there is no genetic penalty to interbreeding, and thus may play a crucial role in species formation by promoting genetic isolation on secondary contact. The barrier is leaky in that occasional errors in song transmission result in misimprinting, which leads to a low incidence of hybridization and introgression. Introgression slows the rate of postzygotic isolation, but can produce individuals in novel genetic and morphological space that can provide the starting point of a new evolutionary trajectory.

Grant, P.R., and Grant, B.R. (1995). Predicting microevolutionary responses to directional selection on heritable variation. *Evolution* **49:**241-251.

Microevolution of quantitative traits in the wild can be predicted from a knowledge of selection and genetic parameters. Testing the predictions requires measurement of the offspring of the selected group, a requirement that is difficult to meet. We present the results of a study of Darwin's finches on the Galapagos island of Daphne Major where this requirement is met. The study demonstrates microevolutionary consequences of natural selection. The population of medium ground finches, Geospiza fortis, experienced size-selective mortality during a drought in 1976-1977; large birds with deep beaks survived better than small birds. During another drought, 1984-1986, the population experienced selection in the opposite direction on beak traits. Changes in food supply were the apparent causes of selection on beak traits in both episodes. As expected from the high heritabilities of all measured traits, the effects of selection were transmitted to the next generation. Evolutionary responses to both episodes of selection were quantitatively well predicted in general. This allows us to conclude that, to a first approximation, targets of selection were identified correctly, and genetic parameters were correctly estimated. Nevertheless, not all responses of individual traits were equally well predicted. A search for possible reasons for the largest discrepancies revealed evidence of bias caused by environmental effects on growth and adult size of some traits, as well as possible selection on the offspring generation before their measurement. These findings illustrate an important assumption in the study of microevolution: that the environments experienced during growth to maturity by the parental and offspring generations are the same, for otherwise a measured difference between generations may have a partly environmental cause, thereby giving a misleading estimate of the evolutionary response to selection. Simple extrapolations from observed selection to long-term evolution may underestimate the total force of selection involved if it oscillates in direction or acts on the environmental variance.

Grant, P.R., and Grant, B.R. (1994). Phenotypic and genetic effects of hybridization in Darwin's finches. *Evolution* **48:**297-316.

Morphological consequences of hybridization were studied in a group of three interbreeding species of Darwin's finches on the small Galapagos island of Daphne Major in the inclusive years 1976 to 1992. Geospiza fortis bred with G. scandens and G. fuliginosa. Although interbreeding was always rare (< 5accumulated for analysis. Five beak and body dimensions and mass were measured, and from these two synthetic (principal-component) traits were constructed. All traits were heritable in two of the interbreeding species (G. fuliginosa were too rare to be analyzed) and in the combined samples of F_1 hybrids and backcrosses to G. fortis. In agreement with expectations from a model of polygenic inheritance, hybrid and backcross classes were generally phenotypically intermediate between the breeding groups that had produced them. Hybridization increased additive genetic and environmental variances, increased heritabilities to a moderate extent, and generally strengthened phenotypic and genetic correlations. New additive genetic variance introduced by hybridization is estimated to be two to three orders of magnitude greater than that introduced by mutation. Enhanced variation facilitates directional evolutionary change, subject to constraints arising from genetic correlations between characters. The Darwin's finch data suggest that these constraints become stronger when species with similar proportions hybridize, but some become weaker when the interbreeding species have different allometries. This latter effect of hybridization, together with an enhancement of genetic variation, facilitates evolutionary change in a new direction.

Grant, P.R., and Grant, B.R. (1992). Hybridization in bird species. *Science* **256**: 193-197.

Hybridization, the interbreeding of species, provides favorable conditions for major and rapid evolution to occur. In birds it is widespread. Approximately one in ten species is known to hybridize, and the true global incidence is likely to be much higher. A longitudinal study of Darwin's finch populations on a Galapagos island shows that hybrids exhibit higher fitness than the parental species over several years. Hybrids may be at an occasional disadvantage for ecological rather than genetic reasons in this climatically fluctuating environment. Hybridization presents challenges to the reconstruction of phylogenies, formulation of biological species concepts and definitions, and the practice of biological conservation.

Schluter, D., Price, T. D., and Grant, P. R. (1985) Ecological character displacement in Darwin's Finches. *Science* **227**: 1056-1059.

Character displacement resulting from interspecific competition has been extremely difficult to demonstrate. The problem was addressed with a study of Darwin's ground finches (Geospiza). Beak sizes of populations of G. fortis and G. fuliginosa in sympatry and allopatry were compared by a procedure that controls for any possible effects on morphology of variation among locations in food supply. The results provide strong evidence for character displacement. Measurement of natural selection in a population of G. fortis on an island (Daphne) lacking a resident population of G. fuliginosa shows how exploitation of G. fuliginosa foods affects the differential survival of G. fortis phenotypes.

Boag, P. T., and Grant, P. R. (1981) Intense natural selection in a population of Darwin's Finches (Geospizinae) in the Galápagos. *Science* **214**: 82-85.

Survival of Darwin's finches through a drought on Daphne Major Island was nonrandom. Large birds, especially males with large beaks, survived best because they were able to crack the large and hard seeds that predominated in the drought. Selection intensities, calculated by O'Donald's method, are the highest yet recorded for a vertebrate population.

Schluter, D., and Grant, P. R. (1984) Determinants of morphological patterns in communities of Darwin's Finches. *American Naturalist* **123**: 175-196.

A procedure is developed and applied to evaluate alternative explanations for morphological patterns in communities of Darwin's ground finches. The first step in the procedure is the computation of expected population density for a hypothetical solitary finch species on an island, as a function of beak depth. This was done for 15 Galapagos islands where food characteristics have been measured. The second step involves construction of hypothetical finch communities for these islands using five different models. Models differ in the extent to which processes of assembly and/or evolution favor species of high expected density, and in the extent to which interspecific competition influences these processes. By comparing predictions of models to actual communities, the roles of food supply and competition could be assessed. Results reveal that expected density is usually a polymodal function of beak depth. Islands differ substantially in the shapes of their density functions. Mean beak sizes of species actually present on each island correspond to local maxima in expected density. However, two species never occupy the same or closely adjacent local maxima. Simple models incorporating the effects of both food supply and interspecific competition on assembly/evolution are shown to accurately predict observed morphological patterns. The results support the hypothesis that both food supply and interspecific competition have determined morphological properties in communities of these finches.