Ecological Character Displacement

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Almost 40 years ago, W. L. Brown Jr. and E. O. Wilson (1) drew attention to a fascinating pattern in the distribution of animals and plants. Closely related species are recognizably different where they live together (sympatry), and virtually indistinguishable where each occurs alone (allopatry). Brown and Wilson called this phenomenon character displacement. Now, on page 798, Schluter (2) reports an experimental test of the character displacement hypothesis applied to a well-documented pattern in nature.

The characteristics that distinguish sympatric species are features such as the beaks of birds, the color of ants, the body size and calls of frogs, and the behavior of fiddler crabs. These or correlated traits function either as ecological tools—in food gathering, for example—or as signals that convey species-identifying information in a mating context. If the species diverged from a common ancestor in geographical isolation, the small initial differences would be enhanced by natural selection when, as a result of climate or other change, the separate populations were brought into contact with each other by an expansion of geographical ranges (1, 3). Why would divergent individuals of the two species be favored by natural selection? Their relative fitnesses would be higher because they would be relatively free from interspecific competition, an ecological advantage, or because they would pair with inappropriate mates either rarely or not at all, a reproductive advantage.

The ecological and evolutionary significance of character displacement was immediately recognized, and additional examples were rapidly found (3). An examination of the fossil record yielded patterns of divergence consistent with a hypothesis of character displacement (4). However, neither the pattern nor the inferred process went unchallenged. Reproductive character displacement fell afoul of both theoretical objections and conflicting data (5), although the idea does have some support (6, 7). Ecological character displacement has not been seriously challenged on theoretical grounds; indeed many theoretical models explore the conditions under which character displacement is likely to occur, and with what consequences (8). Nonetheless, empirical difficulties have been exposed. A vigorous debate has centered on the appropriate statistical procedures to be used for assessing whether a given difference between a pair of species can be attributed to chance or to some biological process such as competition (9, 10). The pattern—any pattern—is subject to alternative explanations, and it requires more than the usual ecological detail to rule out alternative explanations to the hypothesis of character displacement (3). This has necessitated measurement of food supply and diets of the presumed competitors with displaced characters (11–13). The hypothesis has stood the test in some instances (11, 12) but not others (13), although all such efforts are unsatisfactorily indirect as they rely on correlation and plausible arguments.

It is surprising that experiments have not been undertaken to test the hypothesized causal role of natural selection directly, because there are numerous experiments on interspecific competition for food and other resources (14–16), and numerous studies of natural selection in the wild (17). One experimental study of beetles in the laboratory was inspired by models of character displacement, rather than by a particular example of a displacement pattern in nature, and it yielded somewhat equivocal results (8). Schluter has now tested the character displacement hypothesis in species that show pronounced trait variation in nature—stickleback fish.

Two species of threespine sticklebacks (*Gasterosteus aculeatus* complex) occur to-

Darwin's Finches

These birds are one of the original examples of character displacement (1). The medium ground finch, *Geospiza fortis* (**right**), is smaller on Daphne Major Island in the virtual absence of a smaller congener, G. *fuliginosa*, than in its presence on several other islands in the Galapagos archipelago (11, 21), implying a competitive character displacement. A new twist to the story developed a decade ago. The large ground finch, G. *magnirostris* (**left**), began breeding on Daphne in 1983 (22), an El Niño year of exceptional rainfall, after having been present in previous years only in the dry season. During a drought from the middle of 1984 onward, G. *fortis* experienced natural selection on beak dimensions (23). Birds with small beaks survived better than those with large beaks. The effects of selection on these heritable traits were transmitted to the next generation; evolution occurred (24). Selection was associated with an increase in small seed abundance and frequency, and a decrease in large seed abundance and frequency. Change in the characteristics of the food supply are sufficient to account for natural selection (24), but there is an alternative hypothesis: character displacement. *Geospiza magnirostris*, a specialist on large and hard seeds, may have contributed to the decline in abundance of these seeds and thereby to the selective disadvantage of the larger members of the G. *fortis* population that occasionally feed on large seeds (smaller members feed exclusively on small seeds). Darwin's finches are one of many examples in nature that can be interpreted plausibly in terms of character displacement, but experiments are needed to demonstrate a competitive and selective effect of one species on another. The new study by Schluter (2) does just that.

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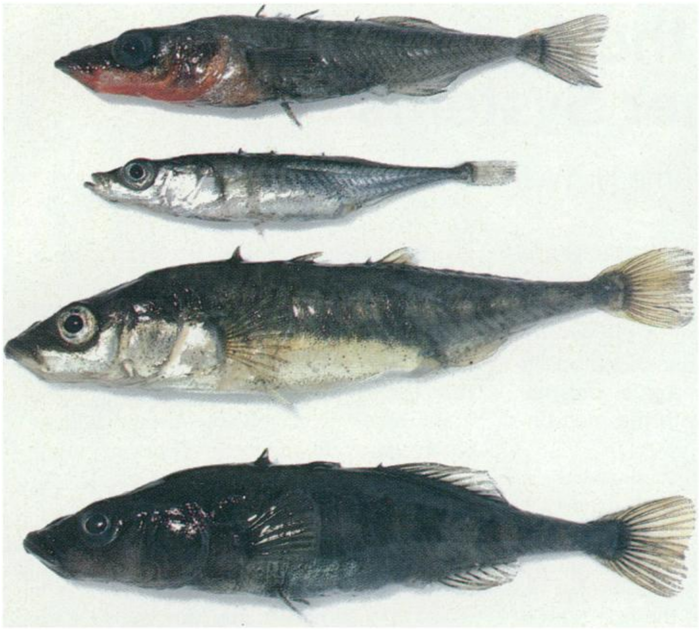

Stickleback fish. From top to bottom, limnetic male, limnetic female, benthic female, and benthic male.

gether in several lakes in the Pacific Northwest (see figure). One, a benthic species, is large and deep-bodied with a few, short gill rakers and a wide mouth. The gill rakers and mouth are suited to its diet, which consists of invertebrates from the littoral zone. The other, a limnetic species, is small and slender and has numerous, long gill rakers and a narrow mouth. It feeds on plankton. When either of these types lives in a lake without the other, it is morphologically and ecologically intermediate. We know this from the pioneering work of Don McPhail (University of British Columbia) and more recent studies by him and Dolph Schluter (*18*). It is just the sort of pattern for which the theory of character displacement has an explanation: Competition for resources, occurring when two previously separated species came together, gave rise to selective pressures that caused evolutionary divergence in food-gathering traits of one or both of the interactants (*19, 20*).

Schluter tested this hypothesis by placing a solitary species in two separated halves of an experimental pond, adding a limnetic species to just one of the halves, and doing the same again in another experimental pond. The replicated experiment thus recreates some of the conditions thought to have been in existence when the two species originally met about 10,000 to 12,000 years ago. It is designed to isolate and expose a possible effect of the limnetic species on the solitary species. (The possibility of a reciprocal effect was not explored.)

Growth and survival of the solitary species were compared under experimental and control conditions to test for competition. If competitive effects are present and size-selective, then those individuals of the solitary species that are most similar to the limnetic species should suffer to a disproportionate extent. Such extreme individuals are naturally rare. Therefore to give the experiment a good chance of working, one extra manipulation had to be made; the frequency of the extreme forms of the two species was artificially increased, by hybridization.

Despite the low power of the statistical tests, a clear difference between treatments was observed. First, the experiment demonstrated a density-dependent effect of competition. Second, within the single generation of the experiment, natural selection occurred. Different solitary phenotypes grew at similar rates when alone, but at different and, on average, lower rates when in the presence of the other species. The crucial result was that the closer they were to the other species in morphology, the lower was their growth rate. Their survival was apparently depressed as well, although the effect was not so marked.

The importance of ecological character displacement lies in what it can tell us about the final stages of speciation, about the manner in which adaptive radiations proceed, and how complex communities develop from simple ones. This experiment is a landmark in the study of character displacement. It not only demonstrates a causal link between natural selection and the presence of an ecological competitor, it opens up a field of experimental inquiry. I hope and expect that there will be many similar studies carried out to test the generality of the findings of this pathbreaking experiment. It remains to be investigated empirically if character displacement occurs widely among organisms, environments, and character systems, or if it is restricted by ecological limitations on the occurrence of competition or by developmental and genetic constraints on responses to selection pressures. If it is restricted, what are the restrictions and why do they operate? New experiments should attempt to go beyond the documentation of natural selection in one generation to the demonstration of an evolutionary response in the next generation. If this can be achieved, then it can be claimed that character displacement, an evolutionary phenomenon, has been established.

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