Finches Show Competition in Ecology

Darwin's finches on the Galápagos Islands were the inspiration for the competition paradigm in ecology; that idea is now rigorously tested

"The major problem confronted by ecologists is to explain the abundance and distribution of organisms," observes Peter R. Grant at the University of Michigan. "There are so many factors influencing the morphology and distribution of organisms that it has been very difficult to generate general theories of community structure." The sharp polarities in the current debate over these questions, and the acrimonious tone in which the debate is occasionally conducted, certainly attest to the extreme complexity of the problem.

Until recently, competition between species, particularly between closely related species, was widely accepted as an important determining factor in the structuring of communities. In recent years, however, this conventional wisdom has been the target of spirited criticism. Because the competition paradigm had come under attack, Grant, in company with a number of co-workers, has been studying the famous finches of the Galápagos Islands with the aim of testing more rigorously than ever before the competition hypothesis.

"Research of this nature on the finches is particularly appropriate," says Grant, "because it was David Lack's classic work, *Darwin's Finches*, that established the foundations in nature of the competition hypothesis in the 1940s." Lack had offered a coherent theoretical framework for understanding the adaptive radiation of the finches throughout the islands, but he had not carried out specific tests of the hypothesis. Grant and his colleagues, Peter T. Boag, Rosemary Grant, and Dolph Schluter, now report that ecological data from three carefully defined situations reveal interspecific competition to have been a major factor, but not the only factor, in generating certain aspects of the communities as observed today.

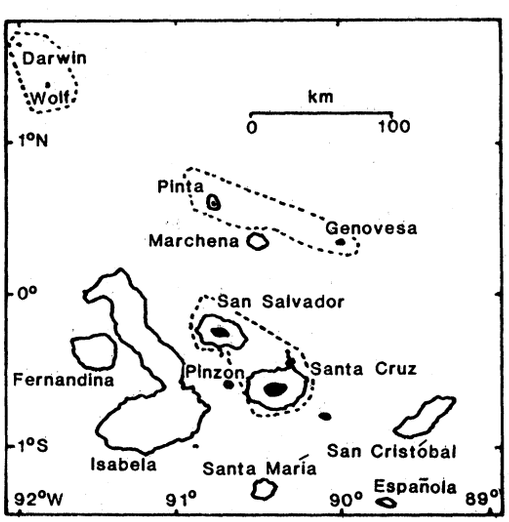
These data and the conclusions drawn from them have met a mixed reception, which reveals something of the nature of the current debate among ecologists. "They go in with the idea that they want to prove competition is important," says Robert Bowman of San Francisco State University. "I can explain their observations by differences in food habits and in environments." Daniel Simberloff of Florida State University acknowledges that competition may have operated in the communities that Grant is studying but argues that this cannot be inferred from the data now available. More pertinent, however, is Simberloff's contention that many of the morphological and species distribution patterns in which Grant and his colleagues are interested are the outcome of stochastic rather than deterministic processes. In which case there is nothing to be explained in ecological or evolutionary terms.

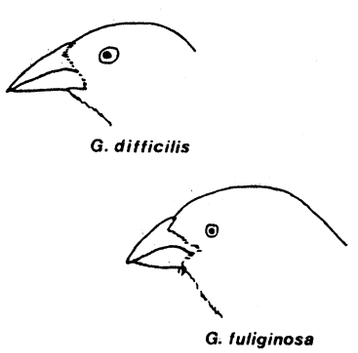
Meanwhile, other ecologists regard the Michigan workers' research as scientifically outstanding and clearly revealing of the importance of competition. "Grant has done some beautiful field studies on the Galápagos finches," observes Jared Diamond of the University of California, Los Angeles. "Some of the studies are classics in this area of investigation." Thomas Schoener, of the University of California at Davis, says, "Before Schulter and Grant's work there was very little good ecological data on the Galápagos finches. They have made more credible the ideas about structuring communities through competition." (The roots of these various differences of opinion are deep and will be the subject of a later article.)

The modern populations of Galápagos finches appear to be the result of an adaptive radiation from a single ancestral species. There is a significant size difference between the different species, of which there are 14 in all and are divided into three major groups. The most marked distinctions, however, are in the size and shape of the bill, which is directly related to the birds' food habits. These food habits, incidentally, vary widely, from seed-eating, through plant- and insect-eating, to blood drinking.

Grant acknowledges that, in the early stages of the finches' radiation, adaptation to different food availabilities was the principle factor influencing the community. As more and more species arose, however, competition became important. What has to be explained, argues Grant, are certain regularities among the populations. Why, for instance, do certain pairs of closely related species rarely occur on the same island, and when they do they are altitudinally separated? And why are some pairs of species more distinctly different in, say, size and beak morphology when they occur together than when they are on islands by themselves? Are such regularities just the simple outcome of differences in food preferences? Or are they result of resource competition?

Working with Schluter, Grant addressed these specific questions to the distribution of two ground finches, *Geospiza difficilis* and *G. fuliginosa*. Of the 25 lowland islands in the archipelago, 20 have only *G. fuliginosa* of this pair, three have only *G. difficilis* and two have neither. The two species do occur on Isla





Map of the Galápagos showing the distribution of G. difficilis *(blackened areas) and* G. fuliginosa *(white areas). Dashed areas show ranges of three* G. difficilis *subspecies.*

Pinta, but *G. difficilis* is principally in the highlands while *G. fuliginosa* maintains its lowland preference, though there is significant overlap in an intermediate zone.

Schluter spent a year doing detailed field measurements on these two species and concluded that currently there is little competition between them on Pinta, even where their zones overlap. "What we are also interested in," explains Grant, "is the possibility that historical competition had generated the pattern we see today." Aspects of historical competition are clearly very difficult to assess, and this has become the focus of the contemporary debate in ecology. "The problem is especially difficult when evolution has taken place as a result of past competition, so that the competition no longer exists. You cannot test for competition directly, but you can test the competition hypothesis through its predictions."

For instance, if unique food preferences alone determined the distribution of these two species then one would predict that for either species food habits would be the same whether the species was on an island by itself or was in the company of the other species. Even if a species' food habits vary according to local conditions, one would still expect the food supply to be different on islands where only *G. difficilis* is present as compared with islands where *G. fuliginosa* exists. By contrast, the competition hypothesis predicts that the two species' food habits will be more similar to each other where they occur on their own than where they coexist.

"The distribution of *fuliginosa* and *difficilis* looks beautifully consistent with the competition hypothesis," says Schluter, "so we wanted a definitive test. I believe we have succeeded" (*1*). Schluter and Grant compared the *G. difficilis* diet on the lowland island of Genovesa and the highland region of Pinta, where it overlaps with a lowland population of *G. fuliginosa*. The diets in these different locations turned out to be different too. Though the birds ate seeds in both islands, the highland Pinta population placed a much greater reliance on insects. Moreover, lowland Pinta was much more similar to Genovesa in terms of its food supply, but this region is occupied by *G. fuliginosa*, a distribution that clearly nods in the direction of competition as a determinator.

The absence of *G. fuliginosa* on Genovesa cannot be explained by any difference between the food supply there and, say, lowland Pinta where the species is present. And neither can the absence of *G. difficilis* from certain other lowland islands occupied by *G. fuliginosa* be attributed to deficiencies in respective food availabilities, argue Schluter and Grant. They present a great deal of data to demonstrate the point and conclude that "the competition hypothesis is supported."

Addressing Simberloff's caveats about stochastic process, Schluter and Grant contend that "We do not see 'randomness' as a very likely explanation for the distribution of *G. difficilis* in relation to *G. fuliginosa*. . . . The probability of such an arrangement is small ($P = .004$)." Simberloff notes that with so many possible combinations of pairs of finch species in the archipelago it is not at all unlikely that a distribution with a low probability will be found, even if the distribution is essentially random throughout.

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Grant's other two recent tests of the competition hypothesis involved different *Geospiza* species. The first, which was carried out with Peter Boag, who is now at the University of Oxford, England, attempted to account for the small beak size of *G. fortis* on the island of Daphne Major (*2*). This species is often to be found on islands with *G. fuliginosa*, but on Daphne Major this second species is absent and *G. fortis* is smaller than usual there. "This is a classic case of character release," says Grant. "Released from constraints of competition with *fuliginosa*, *fortis* shifts to a morphological position intermediate between the two, on a beak size axis and a diet axis."

The second investigation, with Rosemary Grant, looked at the differences in beak size between two populations of *G. conirostris* (*3*). The situation here is much more complicated than, say, on Daphne, but the Grants attribute the beak size difference to competition with *G. magnirostris* in one population, which is absent in the other. They admit, however, that the competition hypothesis does not account for all the distribution observations they make in this study.

Confident that he has demonstrated the importance of competition in contributing to community structure, he nevertheless aligns it with effects of food supply as a complementary influence. "We can understand why species occur where they do, and why those species have beak dimensions and body sizes that they do, largely in terms of two factors. First, the major differences in finch communities between the islands is explained mostly by differences in food supply. Inter-specific competition for that food supply constitutes the second, complementary, factor."

This two-factor explanation has large explanatory power, contends Grant, but is still insufficient by itself. "Other factors, such as parasites, predators, the fluctuation of food supply through time, hybridization between species, and the limited opportunity for dispersal among the islands, all can be locally important. But overall, they are not as important as food supply and competition."

The data, and the conclusions drawn therefrom, come from bird populations in an island archipelago, so how general can they be taken to be? "There is a drawback in studying the Galápagos finches in that the degree of competition there is not likely to be large," observes Diamond. "But if you can demonstrate competition, as Grant seems to have done, then it ought to be even more strongly developed among continental populations where more species are present and at a greater population density."

Grant sees no reason why the process should be restricted to birds in archipelagos since, he says, many of the features that gave rise to the competition hypothesis in the first place are exhibited by other organisms in other environments. "We see this in mammals, insects, plants and so forth. Moreover, there have been a variety of successful demonstrations of competition as a contemporary process, and so I see further justification for concluding that these results on historical competition in the Galápagos finches are probably general."—**ROGER LEWIN**

References

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2. P. T. Boag and P. R. Grant, *Biol. J. Linn. Soc.*, in press.
3. B. R. Grant and P. R. Grant, *Evolution*, **36** 637 (1982).