EVOLUTIONARY ECOLOGY

Theory fits the bill in the Galápagos Islands

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THOSE who criticize the theory of evolution by natural selection often do so on the grounds that it is impossible to test it by making quantitative predictions. Rosemary and Peter Grant now show this view to be wrong[1]. Not only have they observed an environmental change and its effects on the feeding ecology of their study species but they have measured the resultant selective forces and, using previous estimates of the heritability of the traits involved, have predicted the resultant evolutionary changes. Their predictions have been precisely correct.

The Grants' study species was *Geospiza fortis*, one of the ground finches of the Galápagos Islands; this is a family that has contributed much to the study of evolutionary ecology through David Lack's famous book[2] and the subsequent work of the Grants and others. The population on Daphne Major, an undisturbed island of only 0.34 km^2 in extent, has been studied closely since 1976, as has the abundance of the seeds on which the birds depend and other aspects of the island's ecology. During 1982–83 there was a severe El Niño event, perhaps the greatest oceanographic and climate disturbance in the Pacific for a hundred years. It brought eight months of heavy rain, totalling over 1,300 mm (the usual annual total is less than one-sixth of this). Not surprisingly, there were profound effects on the vegetation. In particular, the abundance of large, hard seeds declined substantially but that of small, soft seeds increased tenfold, so that the total biomass of seeds available was much greater. The changes in relative abundance of large and small seeds persisted until at least 1991.

The response of *G. fortis* to the increased food supply was dramatic. The 1982–83 rains gave rise to prolonged breeding. Indeed, some birds that were hatched early in the event were themselves breeding before the end of it. Numbers increased rapidly. Afterwards, with a return to normal, dry conditions, there was no further breeding until 1987. Birds died in the intervening four years, so that only 37 per cent of those alive in 1983 bred in 1987. Furthermore, that 37 per cent did not constitute a random sample — they had longer and narrower bills than the 1983 average. This fits in with observations on feeding behaviour in this species: when small seeds are more abundant, they make up a greater proportion of the diet of the birds (especially of individuals with narrow bills). As expected, there was a marked shift to small seeds during and after the El Niño event.

That the 1982–83 event resulted in marked selection on the bill size of *G. fortis* has been known for some time[3]. The Grants have now updated their measures of selection, predicted its outcome, and tested their prediction. The magnitude of selection on bill width and bill length was measured by comparing the mean values for birds that survived to breed in 1987 with those of the 1984 population. In earlier studies, Boag[4] had measured the heritability of bill width and bill length in this population, as well as the genetic covariance between these characteristics (wide bills tend also to be long). Using standard quantitative genetics theory, it was therefore possible to predict the outcome of the observed selection; that is, the difference in means between the original population and the offspring of those that bred. For bill width, a decrease of 0.13 mm was predicted. In the event, there was a highly significant decline of 0.12 mm — a remarkably close fit.

The prediction for bill length was that it should increase, but only by 0.01 mm as the direct selection for long bills was almost balanced by selection for narrow bills (which tend to be short). In the event, there was a non-significant increase of 0.06 mm in mean bill length.

These results are supported by those for the second species on the island, *G.*

scandens. This feeds on cactus seeds, which declined markedly in abundance after 1983. As a result, there was a substantial decrease in *G. scandens* numbers because this species did not shift its diet; but, precisely because the diet was unchanged, the decline was not selective. No change in bill dimensions was therefore predicted for this species, and none occurred.

As well as contributing to our understanding of evolution, this study has object lessons for the way we do ecology. For too long, even ecology has been dominated by the short-term nature of science funding and by the need, if one is to make a mark in a competitive world, to produce results quickly. Fortunately, the value of long-term studies is now almost universally recognized, thanks to those such as the Grants who have kept such studies going against the odds and who, in doing so, have shown how essential is a long-term approach if we are to have a true understanding of the natural world. □

The finch connection — *Geospiza scandens*, with both female and male, and (above right) a lone *G. fortis*. The illustrations, by John Gould, first appeared in the *Zoology of the Voyage of the H.M.S. 'Beagle'* (1841), and are reproduced from the 1983 reissue of ref. 2.

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1. Grant, B. R. & Grant, P. R. *Proc. R. Soc.* **B251**, 111–117 (1993).
2. Lack, D. *Darwin's Finches: An Essay on the General Biological Theory of Evolution* (Cambridge University Press, 1947).
3. Gibbs, H. L. & Grant, P. R. *Nature* **327**, 511–513 (1987).
4. Boag, P. T. *Evolution* **37**, 877–894 (1983).