

Preface

FIFTEEN years ago a curator of birds at a prominent museum asked me what my next research would be. I told him I was thinking of studying Darwin's Finches, to which he replied "But I thought they had been done!" By this he meant that all the species had been well characterized taxonomically, and a comprehensive interpretation of their evolution had been published by David Lack in 1947, extended by Robert Bowman in 1961, and incorporated into the fabric of modern, general, evolutionary theory (Mayr 1963).

In fact Lack's admirable book had not solved all problems posed by the finches (Wynne-Edwards 1947, Ratcliffe and Boag 1983), nor had Bowman's monograph. A commentary on Lack's book by Richards (1948, p. 84) had, by 1971, lost none of its freshness:

... Mr. Lack's theories come out reasonably well, but there seems to be a permanent dichotomy between those who find their zest in the natural selection theory and those who cannot. The problem, for instance, of whether certain specific characters (e.g. beaks of *Geospizinae*) are or are not adaptive (vague term) is one involving studies of field populations, genetics, and variation. It is a problem which might be largely solved by teams of workers dealing for a number of years with a particularly favourable example. It is not one, I think, which can be settled in a four months stay, even if supplemented by the examination of skins in museums. It is not, of course, that the beaks may not be adapted to different uses, but that it is extremely difficult to prove that this is so to an extent which affects the level of the population.

This book meets the challenge thrown down by Richards. It provides an account, from long-term field studies, of ecological and evolutionary processes occurring in populations of Darwin's Finches over a period of more than a decade. It integrates these processes with the evolutionary patterns so well described by Lack (1947) and Bowman (1961) to produce an explanation for the evolution of the group as a whole. It then compares the adaptive radiation of the finches with several other diverse groups of animals to see how far the finches can be treated as a model of evolutionary diversification.

It would be false of me, however, to imply that I studied Darwin's Finches specifically in order to meet Richards' challenge. The book, and the research that gave rise to it, had different origins. I chose to study the

finches for two, quite different, reasons. The first arose from a confusion about the significance of population variation. Leigh Van Valen had proposed in 1965 that population variation in the size of such traits as the beaks of birds is adaptive, in the sense that different variants in a population occupy slightly different ecological niches and experience slightly different selective forces. He tested this idea with several comparisons involving, among others, Canary Island, Azores Island, and European mainland samples of chaffinches (*Fringilla coelebs*) and blue tits (*Parus caeruleus*). In general he found strong empirical support for the idea. His comparisons were not the most logical, however, and when I performed the proper comparisons I found little evidence to support his views (Grant 1979a, 1979b). Little or no evidence is not the same as contrary evidence, so to investigate a more promising situation in which natural selection could be studied, I asked what are the most variable populations of birds that might be amenable to ecological and behavioral field study? From David Lack's book I knew the answer: Darwin's Finches.

The second reason sprang from a similar confusion concerning interspecific competition. On the one hand, I had just completed a series of field experiments which had demonstrated competition between species of rodents (Grant 1972a). On the other hand, I had taken a critical look at the evidence for character displacement, that is, the tendency for differences between ecologically similar species to be enhanced where they occur together as a result of natural selection having minimized competition between them (Brown and Wilson 1956); the evidence, including that for the so-called classical case of character displacement, looked very weak (Grant 1972b). Therefore I was confronted with this dilemma: competition was a demonstrable process in nature, now, but some of the best evidence for competition as a historical process had crumbled; hence its importance in contributing to the structure of communities was called into question. Since the classical case of character displacement was invalid (Grant 1972b, 1975a), it was logical to turn attention to the classical case of character release. Character release refers to changes in the morphology and ecology of a species apparently resulting from the absence of restraints from a competitor species (Grant 1972b). The classical case involves two species of Darwin's Finches on the Galápagos Islands (Brown and Wilson 1956).

Despite having two good reasons for studying the finches, I might never have begun research on them without the stimulus of a proposal from a prospective postdoctoral Fellow, Ian Abbott. He had developed a plan for detecting the effects of interspecific competition among Darwin's Finches, having been struck by the fact that Lack and Bowman had come to different views about competition from examining the same material. We prepared a research proposal and sought financial support. And here we ran into a prob-

lem that confronts many research workers today. Funds are possible to obtain, providing the project is good, if preliminary data can be marshaled to show that the proposed project has a good chance of being successful. But without funds, how could we get the preliminary data, 6000 miles from home, to show this? We were very fortunate to be funded by the Faculty of Graduate Studies and Research of McGill University, in what must have been partly an act of faith. Had we not received the money we would probably have given up, as alternative prospects looked bleak. I am grateful beyond measure for that initial support.

The first visit to Galápagos in 1973 was an end in itself, and was dominated by the fieldwork of Ian and Lynette Abbott. That I have returned in most years since is due to conversations with Tjitte de Vries, then a member of the staff of the Charles Darwin Research Station on Isla Santa Cruz. At the end of the first visit he pointed out that our work, conducted in the late wet season and early dry season, should be repeated at the end of the dry season when environmental conditions are so different. After I had followed his advice, he persuaded me that no two years are alike, and our research has continued ever since. The book grew out of this continuing research.

I have had the good fortune to collaborate with several enthusiastic and talented people: Ian Abbott, Lynette Abbott, Jamie Smith, Peter Boag, Laurene Ratcliffe, Trevor Price, Dolph Schluter, Lisle Gibbs, Stephen Millington, and my wife, Rosemary. They and I, variously, constitute the "we" used frequently in this book. We have been ably assisted by David Anderson, Chris Chappell, Robert Curry, Phillip deMaynadier, James Gibbs, Erick Greene, Sylvia Harcourt, Margaret Kinnaird, William Johnson, Steven Latta, Douglas Nakashima, Scott Stoleson, Jon Weiland, Michael Wells, David Wiggins, Tom Will, my daughters Nicola and Thalia, and many others to whom I can record my gratitude only collectively and anonymously.

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