BOOK REVIEWS

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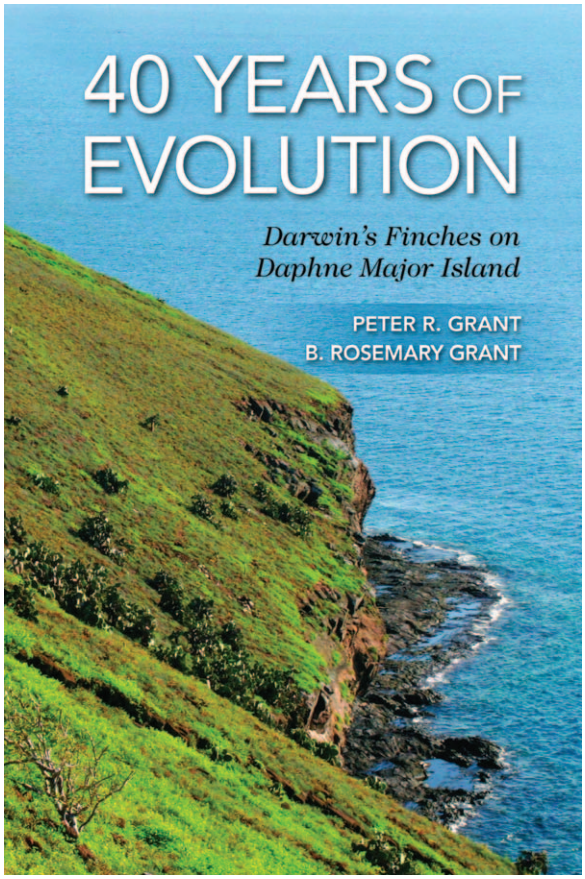
40 Years of Evolution. Darwin's Finches on Daphne Major Island by Peter R. Grant and B. Rosemary Grant. 2014. Princeton University Press. Princeton, New Jersey. xxxii + 400 pp., 175 figures. ISBN 978-0-691-16046-7. Cloth, $49.50.

Research on the Galápagos finches by the Grants and their students and colleagues probably constitutes the most sustained and detailed field study of a single group of species and has illuminated many aspects of evolution. In **40 Years of Evolution**, they summarize the monumental amount of field work, and some associated laboratory work, on the finches of Daphne Major to provide further insights, especially in three areas of evolution that have seen massive amounts of research with the advent and dramatic expansion of molecular genetic tools: rapid evolution, hybridization, and speciation. However, the book is much more than a treatise on what research on this community tells us about the finches or about evolution in general. It is a catalog of the rigors and rewards of arduous and often tedious field research, as well as a description of why long-term field research is necessary and a plea for much more of it. It is also a case study of how research on one apparently straightforward question almost invariably leads to the realization that the question is not so straightforward, and rather leads to other interesting questions.



The speed with which evolution can and often does occur is the most topical of the subjects highlighted in this book, with a recent general treatment by Thompson (2013) that features the Grants' research and a hotly debated popular book by Wade (2014) focusing on human evolution. Nearly twenty years ago, Wiener (1995) won a Pulitzer Prize for a popular book largely about how the Grants' research on the finches of Daphne Major demonstrated the omnipresence and speed of evolution, and **40 Years of Evolution** shows that doubling the length of the study more than doubles the important results, confirming the speed and omnipresence of evolution, showing that sharp vicissitudes are common, and uncovering many of the drivers of evolution as well as their genetic legacies. The two resident finches on this island throughout these forty years were *Geospiza fortis* and *Geospiza scandens*. Because of the sustained and intense field work, the Grants are able to associate particular abrupt shifts in the direction of evolution of both species with particular events, especially drought and the arrival and establishment in 1982 of a population of a new, larger species on Daphne Major, *Geospiza magnirostris*, probably fostered by an early El Niño that year. The major factors driving evolution in this system for *G. fortis*, the species that has evolved the most quickly and to the greatest extent, appear to be which other finch species are present, weather, and which plant species are available in what amounts (which in turn is greatly affected by which other finch species are present and by weather).

It is a commonplace among tourists and even many non-ornithological scientists visiting the Galápagos that all the ground finches look pretty much alike except for size—

black males, brown females, quite nondescript except to aficionados, who notice first and foremost a wide variety of beak shapes. As depicted in the book by copious excellent figures (many in color), within each species there is quite a bit of variation, but in 1973 there was no overlap in beak length between *fortis* and *scandens*, and in 2012 there was a lot. The Grants have shown that one reason the finches are so similar, and one reason each species is so variable, is hybridization. The convergence between *fortis* and *scandens* is partly driven by hybridization between the two species. Because the Grants and their colleagues banded so many birds and observed matings so intensively, they could determine not only which hybridizations occurred but also which offspring were hybrids. Microsatellite DNA analyses reveal some of the genetic consequences. Partly because *fortis* occasionally also hybridizes with immigrants from the much larger nearby island of Santa Cruz of the smaller *G. fuliginosa* (which did not establish a population on Daphne Major during these forty years), *fortis* varies more morphologically than *scandens*. However, the impact of the hybridization on morphology is greater in *scandens*. Detailed records on survivorship show that hybrids are less fit than individuals of the parental species at some times and more fit at others, depending primarily on food availability.

At the limit, hybridization can lead to what the Grants term "despeciation," the merging of two species into one large gene pool, as has happened in some instances with introduced and native species (see, e.g., Rhymer 2006). Although they do not expect this to happen with *fortis* and *scandens* on Daphne Major, they believe this is exactly what happens with occasional propagules of *fuliginosa*, which hybridize inevitably with *fortis* with subsequent backcrossing into the *fortis* population. With regard to the future similarity of *fortis* and *scandens* on Daphne Major, it would have been interesting to confront the Grants' massive data on availability and use of different food plants by the different species (and their hybrids) with the models of Abrams (1990), which predict that, independently of hybridization, competition for food can drive character divergence as well as character displacement.

In addition to despeciation by hybridization, the Grants have observed a remarkable example of the beginning of speciation by hybridization, a new lineage ("Big Bird") established by a hybrid male between *fortis* and *scandens* from Santa Cruz who arrived in 1981 on Daphne Major. Descendants of this individual and a *fortis* female are morphologically distinct, have a distinct song, and are reproductively isolated from *fortis*. In short, they appear to be the beginning of a new species. The Grants predict the lineage will probably not survive, perhaps because of inbreeding, but it is hard not to wish that it does.

The Grants are at pains to emphasize repeatedly the uniqueness of Daphne Major and its finches, even conspecifics on other islands, caused by the particular sets of circumstances—such as habitat mixture, weather, sporadic arrivals of migrants—that characterize each island. Daphne Major is a very small island compared with its near neighbor, Santa Cruz, and several others in the Galápagos. For at least some of these finch species, the Grants and their colleagues have amassed enough information on movement that one can consider the birds of the entire archipelago a metapopulation, and probably the birds of Daphne Major and other small islands act as peripheral populations of a metapopulation of the Boorman-Levitt type (Boorman and Levitt 1973). This raises questions that are not strongly addressed in the book. To what extent does the evolution of these species on Daphne Major affect their evolution in the archipelago as a whole over the long run? Even if the answer to this question were "not much," the evolution and its mechanisms that have been revealed by the Grants' forty years of research are of the greatest interest. However, would they apply largely to very small populations isolated to the degree that these are, or would the same sorts of forces and patterns obtain in a much larger population? Of course, it is entirely possible that incipient species like Big Bird arise frequently, in geological time, and on small islands as well as large ones. If, once in a while, such lineages persist and spread to other islands, could this be the means by which so many species of finches arose in the first place?

Perhaps the most striking conclusion of this book is the overwhelming role of contingency in the evolutionary trajectories of these birds: the confluence of a particular bout of weather with the arrival of a particular migrant, the chance heterospecific mating yielding offspring that happen to be selectively favored by the weather in just that year and few others. It is clear that, as the Grants point out, many different details, and maybe even different main points, might have emerged had they performed this research in a different four decades. The contingency that struck this reviewer most was that a key plant for *fortis*, *magnirostris*, and the Big Bird lineage is caltrop (*Tribulus cistoides*), which was almost certainly introduced since European arrival. The community would likely be very different had this not happened—*magnirostris* would probably not persist, and the evolution of *fortis* size and bill shape would surely have been different.

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