Darwin's Finches: Multiply and Subtract

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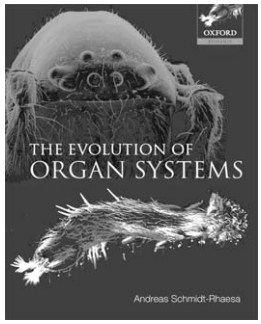
particular conclusion is contingent on taking into consideration all *relevant* evidence. Evidence is relevant, either in a positive or negative sense, if it has an effect on the support for a conclusion. Over the past 20 years, this requirement has periodically received attention in phylogenetic systematics, but for the most part it has either been grossly misinterpreted, vaguely acknowledged, or, more often than not, completely ignored. Schmidt-Rhaesa echoes this lack of concern in chapter 2, where he states that "there are attempts to combine morphological and molecular analyses (total evidence [sic] and other methods).... The different data sources and different analytical tools have led to a wide variety of phylogenetic hypotheses. Such hypotheses are sometimes congruent, but incongruence is a common phenomenon" (p. 3).

Schmidt-Rhaesa does not say how to address this issue, but ironically it is in the last chapter (15), "Final Conclusions," that he writes: "If one is interested in the evolution of structures, organs, and organisms, the aim must be to develop an evolutionary scenario that is as complete as possible" (p. 293). One is left wondering why this latter point of view does not form the basis for the entire book. Schmidt-Rhaesa's compilation of observations from the vast literature is a noble effort. But to speak of the evolution of organ systems is to go well beyond compilations of observations and engage in the synthesis of data. It is as a synthetic work, implied by the title, that the book falls far short of its mark.

The Evolution of Organ Systems has a marked redeeming quality: the exhaustive reviews of metazoan organ systems, including spermatozoa, are the strengths of the book. These reviews clearly hint at the wealth of phylogenetic information that still needs to be investigated. The book shows us that it is the observational realm lying between "morphological" and "molecular" that deserves the greatest consideration. If the goal of evolutionary research is to acquire causal understanding of organisms, then there remains a gold mine of research programs waiting to be tapped below the body walls of the Metazoa. I do wish this book had offered a firmer foundation for promoting such pursuits.



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DARWIN'S FINCHES: MULTIPLY AND SUBTRACT

How and Why Species Multiply: The Radiation of Darwin's Finches. Peter R. Grant and B. Rosemary Grant. Princeton University Press, Princeton, NJ, 2007. 272 pp., illus. $35.00 (ISBN 9780691133607 cloth).

How and Why Species Multiply is an odd book. The title suggests it will review the hows and whys of speciation. The authors, Peter and Rosemary Grant, renowned evolutionary ecologists from Princeton University, execute this task quite well in the classic Mayrian framework, invoking isolation of populations and divergence (either adaptive or neutral) in allopatry, followed by the origin of premating or postmating reproductive isolating mechanisms, and eventual secondary contact, where isolating mechanisms might be strengthened (or eroded). The subtitle, however, *The Radiation of Darwin's Finches,* suggests that Darwin's finches will be used as a case study. This is where things get odd, as there is little about the finches that fits the classic model.

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First, allopatry is only approximate, as the authors have documented numerous cases of interisland dispersal, and in historic times populations have been extirpated and replaced, hardly the norm for speciation in isolation. Second, species overlap in phenotypic space, and many congeners are difficult to tell apart in the field and in the museum. In fact, it is sometimes said that "only God and Peter Grant can identify the finches." This is not unique for birds—there are many avian sibling species—but it is atypical for other clear adaptive radiations. Third, interisland movements have also led to considerable hybridization, and the authors now ascribe a significant role to this in finch evolution. Certainly, differentiation can proceed with ongoing hybridization, given strong countering selection, but it is atypical for other adaptive radiations. Last, molecular data fail to discriminate most of the species in the two main genera (*Geospiza* and *Camarhynchus*), a result reminiscent of cichlid fishes (although their morphology is more clear-cut), but unlike other adaptive radiations of birds. Thus, Darwin's finches are not obvious examples of the standard understanding of how speciation proceeds.

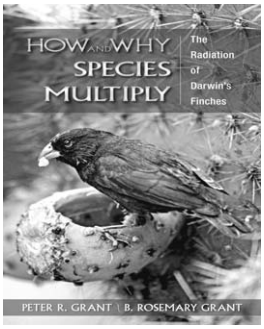
The authors present analyses and interpretations that require a robust phylogenetic hypothesis. The simple fact is that there is no established molecular phylogeny apart from the evidence supporting the groups *Geospiza, Camarhynchus, Platyspiza, Cactospiza,* and *Pinaroloxias,* and two species of *Certhidea* (Sato et al. 1999). Importantly, species limits in the genera *Camarhynchus* and *Geospiza,* arguably the most important of the finches in ecological studies, are not supported by mitochondrial DNA (mtDNA) or microsatellite data. The authors ignore the lack of species-level monophyly and present a tree (plate 1) based on a single exemplar for species in *Camarhynchus* and *Geospiza,* which is misleading at best. The topology of the "tree" in plate 1, however, is not the same as that in figure 2.1. The lack of species-level mtDNA and microsatellite diagnosability is exactly what one would predict from the high level of

interisland dispersal and subsequent introgression that the authors have documented. The species in these genera, if they exist, are not typical of most species in that their boundaries are fluid over time. The authors explain the molecular results by claiming that the finches are at an early stage in speciation, considering them examples of "species before speciation is complete" (p. 155). It seems equally likely that the finches are trapped on a circular conveyor belt, in which natural selection begins the process of species multiplication, but subsequent gene flow subtracts its effects. This could keep the finches perpetually "below" the species level.

The lack of a resolved tree presents other difficulties. For example, the authors claim that the mtDNA tree differs from the microsatellite phenogram in the placement of the Cocos Island finch. The trees might indeed differ, but the microsatellite phenogram (not a phylogeny) is actually unrooted; the authors say it is rooted, but the distance from the outgroup to the ingroup is negative, thereby obscuring this conclusion. The authors present a *ln*-lineage plot (figure 10.2) designed to show the temporal pattern of net diversification (speciation minus extinction). Contrary to the figure legend, however, the plot cannot be reconstructed from their figure 2.1 because that "tree" shows 19 terminal taxa, whereas figure 10.2 shows a maximum of 14.

Figure 11.1 purports to show that Darwin's finches occupy a greater morphological space than do other related groups. However, the finches are now represented by 18 points (not the 14 species assumed by the authors); if one had a similar number of Caribbean taxa represented, the morphological spaces could be equivalent (that is, the appropriate unit might be morphological space per taxon). The evolutionary interpretation of the sequence of speciation (pp. 127–128) is inconsistent with any tree topology presented in the book.

In addition, the legend of figure 10.3 was apparently not proofread, as it perpetuates a common misunderstanding of how trees are interpreted. The authors state that the tree shows that *Pinaroloxias inornata* appears to have evolved from *Certhidea olivacea,* but these two extant species are two nodes apart, and even if they were sister species, trees show that descendant species derive from a common ancestor, not from one of the two species shown as terminal taxa. Thus, evolutionary inferences requiring a tree of Darwin's finches are compromised because of the lack of support for species limits and uncertain phylogenetic relationships.



Nowhere else can one find 30 years of morphological data from birds breeding on a single island.

The authors have done a first-rate job of summarizing three decades of research on the finches. The ecological aspects of the book are quite well presented. The section on colonization of islands is very clear and instructive, and provides a lucid account of how islands might be colonized. The Grants outline their view that adaptive radiations consist of three parts, a stage of ecological divergence in allopatry followed by sympatry, a second stage of genetic divergence, and finally the complete cessation of gene flow, which is said to take at least 7 million years in birds but could take 30 million to 40 million years. They conclude that Darwin's finches are in stage one. The notion that now-submerged islands provided grounds for testing new phenotypes or recombining those already available represents an important insight into the finches' evolution.

Studies of song variation and learning are clearly summarized, as are instances of misimprinting. For example, the authors report a fascinating case in which two female siblings from a nest of *Geospiza fortis* on Daphne Major "mispaired," one mating with a male *Geospiza scandens* and the other with a male *Geospiza fuliginosa.*

The studies of natural selection on beak size are elegantly presented and provide textbook examples. Nowhere else can one find 30 years of morphological data from birds breeding on a single island. These data clearly demonstrate fluctuating selection pressures and concomitant responses by finch beaks. The work on the evolution of beaks at the molecular level constitutes breakthrough research on the developmental genetics of phenotypic differences that have fitness consequences in wild birds.

The book is valuable as a condensed version of the huge amount of fine work the authors have done on the finches. It should be accessible to scientists and informed lay audiences alike. The theory and ecological aspects are very compelling. From the standpoint of evolutionary interpretation, however, the book is lacking. It seems likely that the evolutionary story of the finches is much more complex than previously appreciated. The authors imply that this book is one David Lack would have written had he had their experiences with the finches. But since the days of David Lack, species limits in the finches have not been seriously tested. This, coupled with the lack of understanding of phylogenetic patterns in the group, makes it unclear why the authors persist in clinging to Lack's view of the evolutionary history of the finches despite some compelling evidence to the contrary.

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