The Speciation and Biogeography of Birds

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The Speciation and Biogeography of Birds.—Ian Newton. 2003. Academic Press, Amsterdam. xii + 668 pp. ISBN 0-12-517375-X. Cloth, $75.00.—Thanks to advances in phylogenetic methods and molecular systematics, the fields of speciation and biogeography have advanced at a tremendous pace. For a researcher entering this field, the literature presents a formidable challenge, and a synthesis of research in biogeography and speciation has been sorely needed. Ian Newton's book, *The Speciation and Biogeography of Birds*, is an awkward step in this direction. Part of the awkwardness comes from confusion as to what the book is actually about. The book traverses a large number of issues, from the role of humans in causing extinctions, productivity of marine environments, dry-wet cycles, glaciation, ecological issues (habitat, food, predators, parasites, competition), and migration, to the molecular clock, to mention a few. After reading the book, it is clear that it is not about speciation or historical biogeography; instead, it is a book about ecological biogeography. The lasting contribution of the book is in its summary of avian distributions and natural history, not in the phylogenetic interpretation of speciation and biogeography.

The fields of speciation and biogeography are inherently rooted in phylogenetic reasoning. However, this is not Newton's main area of expertise, which renders some of the sections in Part 1, which focus on "Evolution and Diversity of Birds" misleading. In particular, the sections are grounded in the school of "evolutionary systematics" (e.g. Mayr and Ashlock 1990), which is not the paradigm used by the majority of modern systematists. Thus, we cannot recommend those sections as a general introduction for a student of ornithology or evolution. Newton prefers the Biological Species Concept for its "recognition" of varying levels of diversity, such as superspecies, subspecies, and allospecies. Newton views those taxonomic categories as objective and uses them as a basis for his analyses. However, the monophyly of few of those taxa have been corroborated by phylogenetic analysis, rendering them potentially inappropriate for his intended use. Newton notes that morphological assessments of evolutionary relationships can be compromised by convergence and that DNA characters are potentially more objective. Convergence is indeed a problem with morphological data, but phylogenetic (cladistic) methods are much better able to detect it than the evolutionary systematics that Newton favors. However, Newton also states that molecular phylogenies and molecular clocks might not be trusted because of many untested assumptions. Although certainly true in some cases, it is the morphological assessments—mostly subjective, non-character-based, and precladistic—that are equally, if not more, suspect. Thus, strengths and weaknesses of different types of data and methods of phylogeny reconstruction are not clearly presented. Perhaps not surprisingly, in the entire book, there are only three phylogenetic trees, the most recent of which was published in 1996.

There are several other problems with the treatment of molecular systematics. Newton equates taxonomic rank with genetic distance rather than tree topology. He states that DNA–DNA hybridization is important for "resolution of the older branches" in the avian tree; however, we know of no lab that still uses DNA–DNA hybridization for phylogenetic inference, because it is recognized that sequence analysis is preferable for all depths in the avian tree of life. Newton repeats (p. 500) the common misperception in the literature that microsatellites evolve more rapidly than mtDNA because of a higher mutation rate. It is indeed a result of Kimura's neutral theory that for strictly neutral traits, the fixation rate equals the mutation rate, independent of the population size. However, this is for loci in the same genome. The confusion stems from misunderstanding of "evolve more rapidly." Although some microsatellite loci have high mutation rates and hence many alleles, it does not follow that those loci have a better chance of capturing population isolation than an mtDNA gene tree. The nuclear genome, because of its mode of inheritance, coalesces on average of four times more slowly than does the mtDNA genome.

Several other problems are worth noting. In comparing the number of species in sister clades, Newton states (p. 350) that the clade

with the highest number of species "…has diversified at a faster rate." Slowinski and Guyer (1989) showed that there could be a huge discrepancy in the number of species in sister clades by chance. Without a statistical test of a clear null model, current clade diversity is not necessarily a predictor of speciation rate. The literature on relative range overlaps of sister species, as a means of inferring the geographic mode of speciation, is not dealt with. The lack of discussion of the importance of coalescence theory in phylogeography is also a shortcoming of the book.

Another example of the lack of phylogenetic emphasis is Newton's comparison (e.g. table 11.1) of faunas based on the numbers of shared species. Here, one tallies species shared across different areas and computes similarity values among regions. It has been long recognized that the highest percentage of shared species is not necessarily an indication that those areas are evolutionarily related. True, it is of some interest to know what percentage of species is shared among regions, because it says something about ecological similarities. However, to reconstruct the biogeographic *history* of areas of endemism (the goal of the field of historical biogeography), one must compare cladograms of independent lineages found in the same areas and search for patterns of congruence. This does not emerge from phenetic similarity of species compositions among areas.

Students of modern "comparative biology" will recognize that knowledge of phylogeny is also critical for making inferences about ecological phenomena. For example, in figure 18.5, Newton compares migration in relation to diet in western Palearctic songbirds. "Diet" consists of three categories: insects, seeds, or mixed. Species are plotted irrespective of their phylogenetic relationships, a problem recognized (Felsenstein 1985) but often ignored in comparative ecological studies. Essentially all of the plots and tables in this book ignore phylogeny.

The foregoing is not to say that Newton does not appreciate the fact that a phylogenetic hypothesis can be important in biogeography (and speciation). For example, Newton uses Sibley and Ahlquist's (1990) phylogenetic conclusions derived from DNA–DNA hybridization comparisons. However, known flaws exist in the trees derived from that method; for example, the "adaptive radiation" of Australasian passerines is explained using Sibley and Ahlquist's 1985 DNA–DNA hybridization data rather than Barker et al.'s (2002) passerine phylogeny, which offers a different biogeographic interpretation. Thus, readers must take interpretations with caution, pending revision of the Sibley and Ahlquist tapestry.

The remainder of the book (parts 2 through 6) covers much ground in ecological analyses of species distributions and life histories. In Part 2, the author summarizes "Major Distribution Patterns" that he divides into continental regions, islands, and seabirds. This section is highlighted by excellent summaries of the major biogeographic realms and their endemic faunas. In particular, the summary on seabird distribution patterns is well written and exposes readers to an aspect of avian biogeography that most are less acquainted with. However, those sections are again troubled by overemphasis on taxonomic rank and inattention to recent literature, as seen in table 5.8 (which fails to recognize Rhabdornithidae, yet recognizes Raphidae that is clearly embedded in Columbidae; Shapiro et al. 2002). Part 3 of the book focuses on the "Effects of Past Climate Change." We found that section to be highly informative, detailing histories of various ecological communities and the taxa that currently inhabit them. Part 4 focuses on "Limitation of Species Distributions" and includes an excellent discussion on measurement of species ranges. But again, the section is largely ecological and neglects concepts in range limitation that are more evolutionary (though he is critical of taxon cycles). Part 5 addresses "Bird Movements," specifically dispersal and migration. The book concludes with Part 6 (Conclusions), which simply summarizes the results of each chapter of the book.

Thus, despite its title, the bulk of the book is about ecological biogeography. In that paradigm, one treats species as though they were different colored marbles sampled from an urn with replacement (which is rarely, if ever, true). One compiles lists of species by habitat or ecological attributes independent of their phylogenetic backgrounds. Thus, although the summaries are often detailed, thought-provoking, and interesting, proper interpretation will require a phylogenetic comparative analysis. Still, the work that Newton has done in compiling the basic information will make comparative studies easier.

So long as its shortcomings are recognized, this book has a wealth of information on the distribution and ecological biogeography of birds. Ornithologists would be aided by having it on their bookshelves as a reference for examples of major distributional patterns, island biogeography, apparent habitat limitations, and bird movements. It is not a modern assessment of speciation or historical biogeography. After major revisions to the first section on systematics, subsequent editions could be profitably retitled "A Global Perspective on The Ecology of Avian Distributions."—Robert M. Zink and Andrew W. Jones, *Bell Museum and Department of Ecology, Evolution and Behavior, University of Minnesota, St. Paul, Minnesota 55108, USA. E-mail: rzink@cbs.umn.edu*

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Molecular Markers, Natural History, and Evolution. 2nd edition.—John C. Avise. 2004. Sinauer Associates, Sunderland, Massachusetts. 684 pp. ISBN 0-87893-041-8. Paper, $59.95 (no cloth edition).—This is the second edition of John Avise's survey of how molecular markers are used across organismal biology. How far we have come in a decade! Until it went out of print, the first (1993) edition was probably the most frequently borrowed—and least often returned—volume from my office bookshelf. Describing the many ways molecular tools could be brought to bear on ecological and evolutionary questions and written in a style that illuminated the excitement of pursuing those studies, Avise's first edition was an engaging introduction for upper-level undergraduates interested in a research career or for graduate students searching for research themes.

Despite my open enthusiasm for the first edition, in less than the mean-generation time of a typical seabird, the world of molecular markers has been transformed, making the 1993 edition sorely antiquated. Whole subdisciplines have risen and fallen: basic phylogeography (a term coined by Avise) was all the rage in the early 1990s, but today, journals such as *Evolution* and *Molecular Ecology* have adopted editorial policies that deter descriptive phylogeography, unless it is used to explore broader patterns or theories. Sequencing has eclipsed RFLP-based (restriction fragment length polymorphism) techniques, microsatellites have replaced fingerprinting, the molecular sexing bandwagon has traveled far down the road, and hundreds of genomes have been sequenced (though we are still waiting for a passerine).

Given this background of a rapidly evolving discipline, the big questions in assessing this second edition are (1) has Avise retained the sense of intellectual excitement that made his first edition such a compelling and inspiring read, and (2) how well has the volume adapted to the changing landscape of molecular tools and their myriad applications?

The new edition succeeds on both fronts, with only a few caveats. Its best feature is the five long chapters on particular applications of molecular markers (Individuality and Parentage; Kinship and Intraspecific Genealogy; Speciation and Hybridization; Species Phylogenies and Macroevolution; Conservation Genetics) that make up the bulk of the book. Those chapters cover their respective topics thoroughly, giving example after example of how molecular markers have provided a window onto processes that were otherwise obscure or intractable. They retain the narrative excitement that characterized the first edition, and they are highly