Speciation in Birds

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Book Reviews

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The following critiques express the opinions of the individual evaluators regarding the strengths, weaknesses, and value of the books they review. As such, the appraisals are subjective assessments and do not necessarily reflect the opinions of the editors or any official policy of the American Ornithologists' Union.

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Speciation in Birds.—Trevor Price. 2007. Roberts and Company, Greenwood Village, Colorado. x + 470 pp., 117 text figures. ISBN 0-9747077-8-3. Paperback, $59.95.—To the ornithologist interested in the origin of species, a book devoted to bird speciation is much welcomed, and a synthesis of the burgeoning literature concerning bird speciation is overdue. This book is largely focused on the ecological and behavioral aspects of diversification, and, while its treatment of these subjects is excellent, this focus may disappoint readers expecting to find a thorough review of speciation *per se* in birds.

A shortcoming of the book is that Price never actually settles on a species concept nor defines speciation. In an early section, entitled "The progress towards species," he adopts a standard biological species concept (BSC). Although he makes an attempt to discuss alternative species concepts, he either does not understand lineage-based concepts such as phylogenetic or evolutionary species or does not care to inform the reader of what they really entail. This is unfortunate, because how one views speciation and its study depends 100% on which species concept is used. We recommend the paper by Wiens (2004) in this regard. Cracraft (1983) discussed speciation in relation to the phylogenetic species concept.

Given Price's inclination to follow the BSC, his definition of speciation must be the process by which two taxa attain characteristics, either pre- or postmating, that confer reproductive isolation. Price does not acknowledge the main criticism of this approach, which, as Bush (1982) noted, is that reproductive isolation is a consequence—not a cause—of speciation. That is, many characteristics diverge in allopatry, some of which may ultimately affect mate choice or hybrid viability. This complicates the design of a research program in speciation because of the unpredictability of character divergences and their influence on behavioral or physiological components of reproductive isolation. Also, Price adopts lineage-based species concepts in situations of allopatry, in effect admitting that the BSC is not operational for his study of speciation. That is, he acknowledges that it is hard to discover processes of speciation in such cases, because it is unclear why reproductive-isolating mechanisms would be favored in spatial isolation. Nevertheless, he spends a considerable part of many chapters exploring ways in which reproductive isolation could arise. Price also considers concepts such as reinforcement, character displacement, and hybrid zones, cases of sympatry in which isolating mechanisms might be tested and either enhanced or eliminated. However, again, the major conceptual problem is as follows: why would a trait, selected for mating preferences in a hybrid zone, spread outside the zone where individuals are not challenged by those possessing the alternate state? Although topics are reviewed in a scholarly manner, replete with interesting examples, their relevance to speciation is sometimes unclear. Many chapters would make excellent readings for a course in evolutionary ecology.

This book was not written from the perspective of systematics, so a more apt title would have been "Ecological and Behavioral Aspects of Differentiation in Avian Taxa." The section on rates of diversification is well written and reviews what many feel is a phylogenetic slowdown in avian lineage-diversification through time, though Price ends with a caveat that this result may be an artifact. Price understands the importance of analyzing sister species in making inferences about speciation and recognizes that when comparing two extant sister species, it is difficult to discern whether their differences arose during speciation (however defined) or after speciation. This means that differences between two very old sister species, for example, may have accumulated after they became species, making it difficult to winnow out which specific changes were directly associated with speciation. Because of his use of the BSC, Price does not consider taxa below the level of biological species to be relevant. However, he recognizes that "phylogroups" exist, and we strongly suggest that these are the units one should use when analyzing speciation, because they are closer to a common ancestor than many sister biological species. Plus, one can reconstruct the evolutionary history of phylogroups and then map ecological and behavioral characteristics associated with reproductive isolation on them. This, to us, makes a much more defensible research program in speciation under the BSC (or any other concept).

One of Price's goals is to sort out the "complementary roles of geographical isolation and ecological differentiation in speciation" (page 1). Ecological and behavioral aspects of differentiation are thoughtfully and thoroughly reviewed, though this comes at the expense of an in-depth discussion of geographic isolation and the factors that retard gene flow. For example, phylogeography is

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almost completely ignored. Because it is widely held that ecological adaptation cannot proceed without an initial reduction in gene flow, the genesis of isolation would seem a natural starting point from which to frame a discussion on ecological adaptation. Phylogeography, with its emphasis on patterns of gene flow and population structure, provides that starting point. Isolation, however, is given scant treatment, and even the chapter on geographic isolation and islands is more concerned with the ecological factors of island colonization and extinction than with geographic isolation *per se*.

One troubling part of the book is the extensive use of the molecular clock. Price routinely produces phylogenetic trees that show uniform rates and are calibrated with the much-used rate of 2% sequence divergence per million years (Ma). Although we appreciate the heuristic value of this exercise, putting every tree on a common time scale with a uniform 2% rate runs the risk that someone will take these diagrams and their implied dates seriously. For example, in figure 10.6, he shows a tree of Chiffchaff (*Phylloscopus collybita*) taxa and associated song-differentiation ("regiolects") that, according to the time scale on the tree, evolved in 0.5 Ma. However, later in the book, he notes that regional dialects can arise extremely rapidly, on the order of generations. Because there are so many phylogenies treated in this way, we are forced to conclude that this is a serious problem with the book. Price, we think, is right in concluding that geographic or phylogenetic patterns of mitochondrial DNA variation will correctly reveal the spatial component of lineage histories, but one must acknowledge the potentially large error in dating divergence events with single loci, owing to the stochastic nature of the coalescent process.

Price draws heavily on Darwin's finches to illustrate various principles. However, he does not make a convincing case that these birds are useful for discerning aspects of speciation—rather, they are exceptions to most rules, which he attributes to them being very early in the process of speciation (an odd perspective, given the apparently high degree of morphological variation). He notes that the forms hybridize, that individuals move among islands, and that their morphology responds strongly to different resource peaks. He also notes that mtDNA sequences, which he relies on heavily throughout the book to represent lineage histories, show no differentiation among most species in *Geospiza* and *Camarhynchus*. Thus, using his 2% Ma^{-1} calibration, speciation events could not be dated. Yet, instead of considering the possibility that the taxa in these genera in fact represent transient morphological states that are ephemeral over evolutionary time scales, he persists in the view that these forms are actually biological species, caught early in their history. It is a difficult sell.

The book is excellent at what it does—investigating the roles of ecology and behavior in bird speciation. Price goes well beyond simply reviewing the work of others. He contributes many original ideas and analyses that have not appeared in the scientific literature. Many tables synthesize information on topics that have not been brought together before. The combination of reviewing knowledge and presenting original ideas in excellent prose makes the book easy to read and greatly stimulates thinking on the topics he covers. As an example, one might think that certain situations would always lead to the splitting of one species into two. Price reminds us, however, that if the environment is already filled with ecologically similar species—for example, relatively late in a lineage's radiation—the speciation process may not succeed. So, speciation is not as simple as having the right populations separated by a barrier. His discussion of the relationship between the incidence of feeding innovations and the origin of new taxa is very interesting and deserves further study.

In spite of a few shortcomings and a focus that belies its title, Price's unique perspective and thorough synthesis of a large body of literature makes this book a must-own for ornithologists or evolutionary biologists, from undergraduates to emeriti, interested in diversification. The ideas and concepts are delivered clearly and are often accompanied with exceptional color figures and illustrations. This book should also appeal to many non-academic bird enthusiasts who want to broaden their knowledge of avian ecology and evolution.—Robert M. Zink and Bailey D. McKay, *Bell Museum and Department of Ecology, Evolution and Behavior, University of Minnesota, St. Paul, Minnesota 55108, USA. E-mail: zinkx003@umn.edu*

Literature Cited

Bush, G. L. 1982. What do we really know about speciation? Pages 119–128 *in* Perspectives on Evolution (R. Milkman, Ed.). Sinauer Associates, Sunderland, Massachusetts.

Cracraft, J. 1983. Species concepts and speciation analysis. Pages 159–187 *in* Current Ornithology, vol. 1 (R. F. Johnston, Ed.). Plenum Press, New York.

Wiens, J. J. 2004. What is speciation and how should we study it? American Naturalist 163:914–923.