Bird Coloration. Volume 2: Function and Evolution

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BOOK REVIEWS

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Bird Coloration. Volume 2: Function and Evolution.—Geoffrey E. Hill and Kevin J. McGraw [editors]. 2006. Harvard University Press, Cambridge, MA. 477 pp., 98 color illustrations, 84 line illustrations. ISBN 0-674-02176-2. $95.00 (cloth).

This is the second in a two-volume series on avian coloration; the first volume covered mechanistic issues of production, perception, and measurement, while this volume concentrates on how natural selection shapes the evolution of color. Both volumes have been edited by Geoffrey Hill, well known for his comprehensive work on sexual selection and color in House Finches (*Carpodacus mexicanus*), and Kevin McGraw, a former student of Hill's, and another remarkably productive researcher on avian color. In the preface, Hill and McGraw recount how they originally set out to write, rather than edit, a book on animal coloration in general. After beginning work they decided to cut the project from all animals to just vertebrates, and then to just birds; after another year they decided to farm out most of the topics to other authors, rather than writing the chapters themselves. Hill and McGraw attribute these decisions to the daunting size of the current literature on color: no one book (or even a two-volume set), they argue, could adequately cover the literature on color in all animals, and no two authors could become sufficiently expert, even on just the bird literature, to write an adequate review in a reasonable timeframe. The decision to enlist other authors has resulted in a set of ten comprehensive reviews, covering a logical range of topics on the evolution of avian colors, and all professionally done. The cost of dividing the task among many authors is a certain lack of unity of outlook, some unevenness in style, and a modest amount of redundancy in coverage among chapters.

The study of avian coloration has been overtaken in the last few decades by two revolutions: first, the rise of sexual selection as the dominant theory for explaining the evolution of display characters, and, second, a revamping of methods for studying color, resulting from a fuller realization of the differences in avian and human color vision. The impact of the first revolution is clearly evident in this volume; as the editors remark, "sexual selection is the dominant theme throughout nearly every chapter" (p. viii). Sexual selection is the explicit subject of the substantial chapter on female choice for ornamental coloration, written by Hill himself. Displaying impressive erudition, Hill first pays homage to early work on mate choice based on color in fish, and then reviews approximately 130 studies examining mate choice and color in birds. One lesson that Hill emphasizes is that the source of coloration matters. For example, though both carotenoid- and eumelanin-based colors may influence female choice, females are likely receiving much different information from the two pigment types: male condition from carotenoids, and male social status from eumelanins. Another conclusion, rather surprising given the number of studies reviewed, is that "only the most preliminary phase of research in this field has been completed" (p. 187). Hill's argument is that, even for carotenoid coloration, let alone other pigment types, too few experimental studies manipulating color have been carried out; in this regard he argues that the bird work still lags behind the fish literature.

Another chapter that explicitly considers sexual selection is that by Simon Griffith and Sarah Pryke, on the benefits to females of assessing male color. Here the authors provide a well-written review of the usual categories of possible benefits of mate choice: direct benefits through parasite avoidance or parental care, indirect benefits through good genes, immunocompetence, or genetic compatibility, and so forth. Contrary to Hill, Griffith and Pryke press the conclusion that the source of coloration is not that important to this type of signaling system. Regardless of whether male color is based on carotenoids or eumelanins, the extent or quality of the color is likely to covary with male condition, which in turn is likely to covary with a number of possible benefits to females.

Juan Carlos Senar provides a review of the use of avian color displays as signals of aggression and dominance. Work on this aspect of avian coloration has arisen in large part from Sievert Rohwer's discoveries on status signaling in the Harris's Sparrow (*Zonotrichia querula*), showing that the extent of black plumage patches not only correlates with dominance status, but serves as a signal that affects status. The central puzzle of such systems is why, if receivers accept the signal at face value, signalers do not exaggerate their signals and thus rise in status. Senar favors three alternative hypotheses to explain signal reliability: that the status signal has a physiological cost, perhaps because development of the signal requires testosterone, which suppresses the immune system; that honesty is maintained by social control, whereby legitimate dominants punish cheaters who dishonestly signal high status; and that subordinates actually have equal fitness with dominants, so that cheating is of no advantage. These hypotheses are largely mutually exclusive, and in many cases one or more of them are countered by empirical evidence. Still, it is possible that each explains honesty in some subset of species.

Trond Amundsen and Henrik Pärn discuss coloration in female birds. Here the two main hypotheses are that color has evolved due to inter- and intrasexual selection acting on females, or that female color is a byproduct of sexual selection acting on males. After another thorough review of the evidence, Amundsen and Pärn come down strongly in favor of the former possibility, that female coloration is largely the product of selection acting on females.

Not all chapters are principally concerned with sexual selection. In one of the best-written chapters, Rebecca Kilner reviews coloration in nestling birds, which, though often drab, sometimes have colorful mouthparts, plumage, or skin. Some of these colors signal the offspring's need or health to its parents, again raising issues concerning signal reliability and its maintenance. Gary Bortolotti discusses functions of avian coloration under ordinary natural selection, explicitly excluding sexual selection functions. Here the possibilities include not only that coloration affects vulnerability to predation, but also that selection is due to ''nonoptical'' effects of color, such as thermoregulation and protection from abrasion.

Although the impact of the sexual selection revolution is seen in most chapters, the effects of the second, methodological revolution are less apparent. Changes in the methods for analyzing color were necessitated not so much by new evidence on differences between human and avian color vision, but by a better understanding of the implications of differences that were already known. If birds use a larger number of cone types than we humans do, and if the sensitivity of those cone types extends down into what humans label the ultraviolet, then assessments made by humans of avian colors may not parallel the assessments made by the birds themselves. Consequently, new, objective methods for assessing colors were needed, based on measuring reflectance spectra. Where these new methods have obviously made a difference is in showing the importance to communication of UV reflectance patterns, most importantly in mate choice (Hill's chapter), but also in offspring–parent communication (Kilner's chapter) and status signaling (Senar's chapter). Whether the new methods have forced the revision of previous ideas about communication via colors in the human visual range is less obvious; perhaps human subjective judgments are sufficient to assess such colors after all, at least for many purposes. The chapter in the present volume that best makes a case for the importance of the new methods of measuring color is that by Ian Owens on interspecific variability. Owens argues that objective, quantitative measures of color greatly facilitate comparative analyses, enabling us to discern the importance of factors such as light environment to the evolution of species differences in coloration.

In conclusion, this volume provides a series of solidly informative, up-to-date reviews that should be extremely useful to any ornithologist interested in avian colors from the standpoint of animal communication and behavioral ecology. Not all the chapters are exciting to read, but one can learn a great deal from any of them.—WILLIAM A. SEARCY, Department of Biology, University of Miami, Coral Gables, FL 33124. E-mail: wsearcy@miami.edu