BOOKS: ECOLOGY

History Explains Avian Patterns

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In virtually all aspects of their biology and behavior, birds are an amazingly diverse group of organisms. For example, body mass in birds varies by a factor of 40,000 between the largest and smallest species, egg mass by 6000, and the period of time between hatching and fledging by 50. Social behavior is equally variable: in some species, males and females mate for life and offer extended care to their offspring; in others, males and females interact only during copulation, and offspring never encounter or interact with their parents. Study of this variation has been critical in the development of ideas in many areas of biology, from speciation and population regulation to animal communication and female mate choice.

Evolutionary Ecology of Birds
Life Histories, Mating Systems and Extinction
by Peter M. Bennett and Ian P. F. Owens

Oxford University Press, Oxford, 2002. 292 pp. $85, £49.50. ISBN 0-19-851088-8. Paper, $45, £24.95. ISBN 0-19-851089-6.

David Lack, in his book *Ecological Adaptations for Breeding in Birds* (Methuen, London, 1968), was one of the first biologists to seek evolutionary explanations for this variability in avian ecology, using what has become known as the comparative method. Lack realized that many important questions in evolutionary biology cannot be approached with standard experimental or observational methods. If one wants to know whether there is a relation across species between the average longevity of individuals and their age at first reproduction, one cannot answer the question by experimentally altering longevity or reproductive age. Applying the comparative method, however, one can test for a statistical association between such variables. The procedure for doing so has changed greatly from the time of Lack, but the essence remains the same: to examine the distribution of traits across taxa (or, more accurately, the distribution of evolutionary transitions in traits) in relation to their evolutionary history, i.e., phylogeny.

Peter Bennett and Ian Owens are two of the major champions of the comparative method. In *Evolutionary Ecology of Birds*, they re-examine the issues that concerned Lack using modern statistical methods and phylogenetic information not available to him. In addition to examining the evolutionary origin and diversity of life-history traits and mating systems in birds, they also consider questions not addressed by Lack, such as the factors that influence the vulnerability of bird species to extinction.

Although the book offers few new analyses beyond those published by the authors over the last decade, putting them all in a single book is itself a valuable contribution, especially because the work constitutes an update to Lack's book. And though none of the analyses reverse Lack's conclusions (that much of the diversity of birds is related directly or indirectly to ecological factors), application of the modern comparative method substantially refines our understanding of the interaction between evolutionary history and ecology.

For example, despite instances of substantial population- or species-level variation in life-history traits, most of the variation in birds occurs between families within orders and between orders within the class. This pattern suggests that most of the currently observed variation is due to changes and adaptations that occurred in the ancient history of the group. Surprisingly, the authors' analyses do not suggest that diets, foraging habits, or developmental modes were the major factor that initiated much of the early radiation in birds; their findings point to nesting habits (e.g., holes versus open nests, and colonial versus singular nesting) as the critical factor. Early evolutionary changes in nesting habits appear to have been followed by changes in mortality patterns, growth rates, and delayed breeding—changes that led to much of the diversity found in extant birds. Current interspecific ecological interactions (such as diet, habitat, and competition) may influence the differences between populations of the same species, but appear rather unimportant when considering the broad differences between major groups of birds.

The most important change in our understanding of avian ecology since Lack's synthesis concerns mating systems: whether individuals live and reproduce with just one member of the opposite sex or are promiscuous in their mating habits. As a result of the advances associated with DNA fingerprinting, which were unavailable to Lack, the historical view of birds as reproductively monogamous is now known to be largely incorrect. Regardless of their social mating system, males and females of most species are reproductively promiscuous. Evolutionary analysis of mating system variation again suggests that diversification early in the history of birds is important in explaining why some species live or mate monogamously and others do not. For example, species with "fast" life histories (high mortality and high annual reproductive rates) are more likely to exhibit non-monogamous mating systems, extra-pair paternity, and intraspecific brood parasitism (females laying eggs in the nests of other females). The authors argue for a hierarchical view of avian mating systems, one in which changes in the life history of groups early in their evolutionary history led to much of the current variation in mating systems, and fine-scale variation between populations or closely related species is related to current ecological interactions.

The comparative method is not without its critics. And, as with any methodology, the results of comparative studies are only as good as the data on which they are based—in particular, the accuracy of the phylogenies. In addition, the separation of cause and effect is often difficult in comparative studies. Despite these caveats, data summarized in *Evolutionary Ecology of Birds* strongly suggest that to explain the adaptive radiation of birds, we must consider their evolutionary history at least as much as we consider their present-day ecological relations. I think that David Lack would applaud the contributions that Bennett and Owens have made to understanding this interaction.

CREDIT: BRIAN PATTESON

Frequent fliers. A Manx shearwater (*Puffinus puffinus*) banded in 1957 was recaptured in early April while preparing to breed on a Welsh island. Probably fifty years old, that bird has covered an estimated 5 million miles on feeding flights and its annual migration to the South Atlantic.

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