

Physiological Adaptations for Breeding in Birds.

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strong sustainability (i.e., specifying what should be protected in nature) and variations thereof, through which he accepts economic sustainability as necessary but supplements it with independent criteria articulated outside the sustainability framework. He also cites ecological resilience as an independent conservation principle, but this has been embraced by most strong-sustainability theorists as a noneconomic aspect of sustainability.

In chapter 8 (“Justice and equity”), the discussion is strongly weighted toward concerns that environmental problems, and even environmental solutions, may fall heavily on the most vulnerable parties affected. The topics in this chapter include responsibility for climate change, environmental racism, social and political ecology, and ecofeminism. Sarkar asks, “Where does this leave us?” in a short, final chapter and closes with a “take-home message for environmental activists that the future they envision can only be achieved if natural values are embedded into the cultural fabric of a region” (p. 199).

BRYAN G. NORTON

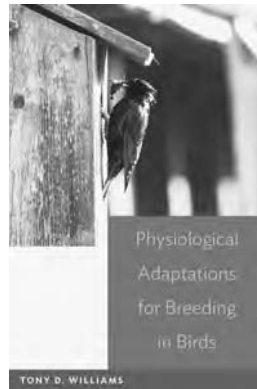
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WHAT DO WE REALLY KNOW ABOUT AVIAN REPRODUCTION?

Physiological Adaptations for Breeding in Birds. Tony D. Williams. Princeton University Press, 2012. 368 pp., illus. \$69.50 (ISBN 9780691139821 cloth).

The title *Physiological Adaptations for Breeding in Birds* will prompt readers with a background in ecology and evolution to recall David Lack’s

highly influential 1968 book *Ecological Adaptations for Breeding in Birds*, in which he provided many of the theoretical foundations for modern evolutionary ecology. Lack’s focus on the ecological and environmental factors influencing the numbers of chicks raised by free-living birds deliberately excluded any considerations of physiological adaptations. In this new book, Tony D. Williams, professor of biological sciences at Simon Fraser University, examines how more recent knowledge of physiological and energetic mechanisms can be applied to the fundamental questions that Lack raised almost 50 years ago to explain individual phenotypic variation in reproductive life-history traits.



Physiological Adaptations reflects the recent awareness of a need for avian reproduction research to become more integrative and multidisciplinary. Historically, evolutionary and ecological approaches have tended to lack consideration of mechanistic constraints. However, physiological approaches have generally not taken into account how the evolutionary selection of mechanisms interacts with the environment to influence lifetime reproductive success. Williams has been a pioneer of integrating physiology with ecology and evolution in the study of avian reproduction. With his education in the United Kingdom and graduate work on the endocrine mechanisms underlying avian seasonal breeding, Williams undertook postgraduate work in the South Atlantic, with the British Antarctic Survey, during which

he developed an interest in the ecological and behavioral aspects of penguin biology. His research in Canada is now focused on egg formation and laying in birds. Williams played an influential role in the international E-BIRD network (not to be confused with the similarly named eBird program), which ran between 2004 and 2008, with the aim of bringing ecologists and endocrinologists together to stimulate collaborative work. As he acknowledges, this project provided an important intellectual stimulus for writing the book.

The evolutionary emphasis of *Physiological Adaptations* is apparent in the organization of its chapters into the key reproductive life-history traits of the timing of breeding, egg size and quality, clutch size, incubation, and parental care. A further chapter considers the tradeoffs and carryover effects of reproduction on other life-history stages. Williams uses a consistent structure within each chapter, considering for each trait the extent of its variation in an evolutionary context before addressing the physiological and energetic mechanisms that may contribute to that variation. He places an emphasis on female reproduction, arguing that the life-history traits having the greatest influence on lifetime reproductive success are ultimately determined by a female’s decision on when to lay her eggs and how much to invest in them. For this reason, a primer is given in an early chapter on the physiological control of egg production.

The tandem focus on both the physiology underlying individual trait variation and the physiology of female reproduction is a continuous narrative throughout the book. A consequence, however, is that *Physiological Adaptations* does not provide a comprehensive treatment of avian reproduction. Readers would need to look elsewhere for an overview of male reproductive physiology equivalent to the one Williams gives for females. He also offers limited coverage of social

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behavior, and many of his examples are, by necessity, only of those species with sufficient life-history traits and physiological data available for evaluation.

Williams does succeed at stimulating critical analysis and discussion of the field, in part by providing a list of future research questions at the end of each chapter. His text combines targeted, well-explained background information with a critical appraisal of current and past research and is illustrated with a range of black-and-white figures from the literature, most of which have been redrawn especially for the book. Thus, *Physiological Adaptations* is an excellent resource for seminar discussion and other question-led teaching at advanced undergraduate and graduate levels.

The most stimulating aspects of the book are the author's refreshingly direct opinions and approach to writing. He does not hide his frustrations concerning many aspects of the current state of avian reproduction research and is equally critical of the more traditional physiological and ecological approaches. Much of what is known about the mechanisms of yolk synthesis in birds, for example, has been derived from work on poultry in which estrogen-treated roosters were used, rather than hens. (The advantage for physiologists, of course, is that the male liver is highly responsive to estrogens and therefore provides a "cleaner" background for experiments, because endogenous estrogens are low in males.) However, studies of females are essential when there is a need to understand the physiological basis of variation in reproductive traits.

From the point of view of physiology, it is striking how mechanistic explanations that appear well established in poultry often begin to break down when they are tested in wild species. For instance, it has been predicted, on the basis of poultry studies, that the maternal hormone prolactin plays a key role in reducing clutch size and promoting incubation; however, this evidence has not been well supported in the limited

number of nonpoultry studies that have been performed. Williams also expresses his exasperation about the persistence in the literature of certain widely held assumptions, despite little direct experimental evidence for those assumptions—for example, how egg production is demanding in terms of the energy and nutrients required. Although recent progress has been made with regard to integrating the physiological and ecological approaches to this research, the overall effort has not been well focused. Much work has been performed on variation in egg size and quality and on the possible underlying mechanisms, such as the deposition of yolk steroid hormones, but there has been little payoff in terms of evidence of long-term effects on offspring phenotype and fitness.

The effect of Williams's critical approach to writing *Physiological Adaptations* is an emphasis in the book on the lack of core knowledge in this research field, particularly in wild species, and especially in females. The central question that the author poses about the extent to which mechanistic variation can explain phenotypic variation in the life-history traits of avian reproduction remains largely unexplored, owing to the limitations of past research approaches. The book's value then lies in its emphasis on the need for the rigorous formulation and testing of research questions. However, for more rapid progress, better integration with emerging genetic and genomic approaches will also be required. As Williams points out, avian reproductive genomics is still in its infancy, but progress is beginning to be made with the availability of next-generation sequencing and the development of DNA chips for analyzing single-nucleotide polymorphisms in wild bird populations. The challenge will be in linking genotypic and phenotypic variation across very large data sets and ensuring that the information is applied effectively and critically to address the fundamental questions raised in Lack's book.

There is much to do before a book on genomic adaptations for breeding in birds can be published. In the meantime, Williams's book provides a rousing stimulus to the field and will provoke established and developing researchers to question what they really know about avian reproduction.

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