Ecological and Environmental Physiology of Birds

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BOOK REVIEWS

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Ecological and Environmental Physiology of Birds.—J. Eduardo P. W. Bicudo, William A. Buttemer, Mark A. Chappell, James T. Pearson, and Claus Bech. 2010. Oxford University Press, Oxford, UK. 328 pp. ISBN 978-0-19-922845-4. $65.00 (paperback).

This book is part of the Ecological and Environmental Physiology series from Oxford University Press, the goal of which is to provide "an integrated overview of the ecological and environmental physiology of key taxa" and "a state-of-the-art review and synthesis of topics that are relevant to how … organisms have evolved and coped with the environmental characteristics of their habitats" (p. vi). To this end, the current volume on birds is divided into nine chapters, beginning with an introductory chapter describing the general body plan of birds and their capacity for flight. Chapter 2 considers general physiological principles that are relevant to describing physiological adjustments to ecological and environmental demands. Chapters 3–7 provide the bulk of the material on how the physiology of birds is matched to ecological and environmental demands and include discussions of the physiological bases for fecundity/longevity trade-offs (Chapter 3), physiological adaptations for obtaining and processing food (Chapter 4), adaptations to specific environments (Chapter 5), neural and sensory responses (Chapter 6), and development (Chapter 7). The book ends with chapters on approaches and techniques used in avian ecological or environmental physiology research (Chapter 8) and conclusions and suggested directions for future research (Chapter 9). An extensive and useful bibliography and an index constitute the accessory materials accompanying the text.

To set the stage for later discussions of ecological and evolutionary physiology in birds, Chapter 1 covers the evolution and phylogeny of birds, the evolution and energetics of flight, migration and flightlessness, and focuses on the general capacity for flight in birds. The authors note the important effects that the capacity for flight exerts on the general anatomy and physiology of birds as a group. The section on bird phylogeny brings up the interesting controversy surrounding the incongruity of the timing of the evolution of the Passeriformes between the fossil record (suggesting a mid-Tertiary radiation) and molecular-clock data (suggesting diversification in the late Cretaceous), but it fails to mention a recent paper that helps to resolve the differences between the two viewpoints and suggests that a Tertiary radiation of the Neoaves is consistent with both fossil and molecular data (Ericson et al. 2006).

In Section 1.8.6, on adaptations to migration, the authors focus on a study showing elevated capacity for oxidation in flight-muscle cells of Semipalmated Sandpipers (*Calidris pusilla*) during migration, which is associated with a concurrent increase in n-3 polyunsaturated fatty acids in muscle-membrane phospholipids. The authors imply that such an adjustment, which helps support elevated aerobic capacity during migration, is typical for migratory birds. Indeed these data are consistent with data from several other studies, but a number of other studies have failed to demonstrate elevation of the aerobic capacity of flight-muscle cells with migration in several species, including the Semipalmated Sandpiper (e.g., Marsh 1981, Driedzic et al. 1993, Weber and Piersma 1996). Thus, enhanced cellular aerobic capacity of flight muscles during migration is not a universal component of the migratory phenotype in birds.

Chapter 2 serves as a good and accessible description of the physiological principles involved in gas, heat, water, and ion exchange between animals and their environment. The chapter is organized around the environmental variables important to birds and, therefore, is perhaps the part of the book most clearly focused on environmental physiology. I only had a couple of minor quibbles with the information presented in this chapter. One, no figures of metabolic rate vs. ambient temperature or avenues of heat exchange between animals and their environment are provided, and these are standard figures for general books covering these topics. Second, the allometric relationship between body mass and metabolic rate is described well in the chapter, but the authors don't discuss the various hypotheses for why the allometric exponents are what they are, despite a flurry of recent work on this topic.

The physiological underpinnings of fecundity/longevity trade-offs are the focus of Chapter 3, which devotes considerable space to the energetic costs of reproduction, including those of egg production. Trade-offs between life history and immunity and oxidative stress in birds are vigorous areas of current research, and the trade-offs between these physiological features and reproductive output are prominently featured in this chapter, which serves as an excellent introduction to and review of these topics. The influence of testosterone on the energetics of breeding males is another topic covered prominently in this chapter. Birds often lose body mass during the reproductive period, and one topic treated in this chapter that was particularly interesting to me is the relation between mass loss and reproductive activity. Two hypotheses explaining the loss of mass during reproduction have been proposed, the reproductive-workload and adaptive mass-loss hypotheses (e.g., Golet and Irons 1999). Within this chapter, the authors proffer the idea that the costs of egg production, which can reduce the mass of flight muscle and heart, impair flight performance and reduce subsequent fitness. The alternative hypothesis of adaptive mass loss to reduce weight for energy conservation during feeding flights is not specifically mentioned. The authors also favor the physiological-constraint hypothesis for the evolution of clutch size in birds over Lack's hypothesis (i.e., clutch size reflects the number of young the parents are capable of provisioning), and they provide supporting evidence from numerous studies demonstrating reduced fitness in females forced to lay extra eggs.

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Chapter 4 treats digestive adaptations to diet and energy demands and provides a comprehensive and synthetic overview of the ecophysiology of digestion. This is, perhaps, one of the most comprehensive chapters in the book and will serve as an excellent departure point for further studies in this area. Phenotypic plasticity and phenotypic flexibility of the digestive system, as they relate to changes in diet and energy demands, are prominent topics of this chapter. This chapter presents more mechanistic physiology than most of the others, treating digestive enzyme function, absorption rates, retention times, and their relative contributions to overall digestive efficiency. Of particular interest to me was the conclusion that the primary adjustment to increased energy demand (from cold-acclimation studies) is an increase in the mass and volume of the gastrointestinal tract while retention time, mass-specific rates of amino acid uptake, and overall digestive efficiency remain unchanged.

The main coverage of environmental physiology in the book occurs in Chapter 5, where adaptations to arid environments, low temperatures, high altitudes, and marine environments are discussed. Much of my own work is centered on avian physiological responses to increasing energy demands associated with cold temperatures, so this chapter was of high interest to me. In general, the authors do a nice job of summarizing organismal responses to environmental variation in this chapter, although I found the level of coverage to be rather cursory. I also had a few quibbles with some of the chapter's information. For example, the authors state that "shivering thermogenesis is able to increase total heat production by roughly 5-times the level of BMR [basal metabolic rate]" (p. 148) and that heat production during shivering is "4-5 times BMR" (p. 152). This metabolic expansibility during shivering is a little on the low side for birds, as capacities for heat production in birds typically exceed BMR by four- to eight-fold (Swanson 2010), with a maximum value of nine-fold in winter-acclimated House Sparrows (*Passer domesticus*) from Wisconsin (Arens and Cooper 2005). In addition, the section on metabolic adjustments to low temperatures focuses on adjustment to BMR, which has received considerable study in birds, but peak cold-induced metabolic rates are likely more directly relevant to cold acclimation (Swanson 2010), and adjustment of peak cold-induced metabolic rates are not discussed in this chapter. The authors also mention the discovery of an avian uncoupling protein (avUCP) and suggest that it may be involved in non-shivering thermogenesis in birds, although recent studies suggest that avUCP may serve an anti-oxidant function rather than, or in addition to, a thermogenic function (Mozo et al. 2005, Rey et al. 2010). I was also disappointed that the authors did not mention seasonal phenotypic flexibility of organismal metabolic rates, which is the primary seasonal adjustment of birds, especially small birds, to seasonal cold exposure, and the seminal works of Dawson and colleagues on cardueline finches (e.g., Marsh and Dawson 1989) are not discussed or cited. Finally, in the section on altitude adaptation, the authors imply that birds' blood generally has an oxygen-binding affinity higher than that of mammals and suggest that this contributes to their relative success at high altitudes. Although altitude-adapted birds do have an oxygen affinity higher than that of birds from lower altitudes, oxygen affinity in bird blood is generally lower than that in similarly sized mammals (Butler 2010).

Neural and sensory adaptations in birds are the topic of Chapter 6, which covers the avian brain, olfaction, vision, magnetoreception, and vocalizations. The introductory section of this chapter discusses brain homologies in birds and mammals and argues that birds have capacities for higher learning comparable to those of most mammals. In this section, the authors use numerous terms relating to brain anatomy that may not be familiar to many readers, so I thought that better definitions of these terms should have been included. In addition, the caption of figure 6.1, which illustrates homologies between bird and mammal brains, has the brains reversed from the actual figure, which doesn't help the reader to follow the discussion of brain homologies. The section on olfaction emphasizes recent findings that birds are capable of using olfaction for a variety of functions, contradicting the common dogma that birds generally have poorly developed olfactory abilities. I found the summary of results on photoreceptors, free-radical pairs, and magnetic reception particularly interesting, although the authors concentrate on this mechanism for magnetic reception and give less attention to the magnetite system.

Chapter 7 covers developmental physiology and examines the growth of embryos and hatchlings, temperature and humidity tolerance, and energetics. Regarding temperature tolerance in chicks, I found the authors' conclusion that chicks' tolerance of hypothermia varies considerably among taxa and that such variation probably reflect adaptation to the irregularity in the rate at which chicks are fed in these taxa very interesting. I wonder whether the variation in hatchlings' tolerance of hypothermia could be functionally related to capacity for torpor in adult birds. I thought that the chapter could have provided a more detailed treatment of the mechanistic physiology relating to the ontogeny of thermoregulation in hatchling birds. The chapter concludes with an excellent and highly useful discussion of the evolution of developmental strategies in birds and the effect that the ontogeny of thermoregulatory capacities plays in this evolution (i.e., the growth-rate-maturity hypothesis).

In Chapter 8 the authors describe many of the modern techniques used in avian ecological and environmental physiology, including methods for measuring metabolic rates in the field, movement patterns, and flight-energy requirements. The authors also provide a brief, but helpful, overview of functional genomic and molecular-biology techniques and their application to ecological and environmental-physiology questions. The authors confine their discussion of measurement of field metabolic rate (FMR) to doubly labeled water and the more recently developed techniques for heart-rate monitoring; they don't mention the use of time-activity budgets for FMR measurement. The level of detail in the discussions of doubly labeled water and heart-rate measures of FMR is substantial, and these sections will be of great benefit to those seeking to incorporate these methods into their research. The section on flight-energy requirements very nicely compares the mass-loss, oxygen–consumption, and heart-rate-monitoring techniques for determining metabolic rates during flight. The short concluding chapter suggests that among the promising avenues for future research is the emerging field of conservation physiology, integrating the study of avian ecological and physiological responses to climate change.

In general, I thought that the topics covered, the supporting examples, and the concentrated focus on specific studies throughout the book were somewhat eclectic, which is perhaps not too surprising for a multi-authored volume. As a consequence, this book does not provide a fully comprehensive treatment of avian ecological and environmental physiology. The authors did an excellent job of covering numerous aspects of avian ecology and ecological physiology, but environmental physiology, in my opinion, did not receive the same level of coverage. In fact, there was more coverage of straight

behavioral ecology than I was expecting. For example, a 35-page chapter was devoted to the important topic of digestive physiology, but only 33 pages total were devoted to adaptations to deserts, cold temperatures, and high altitudes, central topics in environmental physiology. In addition, though 15 pages were devoted specifically to the nervous system, only five address migration specifically, and only one covers adaptations to migration. Moreover, there is no specific chapter covering avian energetics, although this material is scattered throughout several other chapters. The book's coverage of organismal physiology is generally outstanding, but mechanistic physiology is not its strong focus, outside of the aforementioned chapter on digestive physiology. Despite these minor shortcomings, this volume provides a very strong overview and synthesis focusing on organismal physiology in birds and on how organismal physiology is adjusted to meet ecological and environmental demands. The book serves as a valuable contribution to the literature on ecological and environmental physiology in birds and will help to stimulate future research in this area. As such, the book will be a useful reference for both upper-level undergraduate and graduate students and professionals working in avian ecology and physiology. However, it doesn't serve as a truly comprehensive source for avian physiological responses to environmental variation, so other sources will be required to supplement this text for a comprehensive treatment of the environmental physiology of birds.—DAVID L. SWANSON, Department of Biology, University of South Dakota, Vermillion, SD 57069; E-mail: david.swanson@usd.edu.

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Shorebird Ecology Conservation and Management.—Mark A. Colwell. 2010. University of California Press, Berkeley. 328 pp. ISBN 978-0-520-26640-7. $60.00 (hard cover), $48.00 (Adobe E-book), $38.40 (Kindle).

It is not often that one picks up a book and realizes he (1) has been missing it for years without realizing it, (2) knows several others who should immediately read or refer to it, and (3) wants to flog it widely within his community. This was the experience I had on examining my copy ordered pre-publication of Mark Colwell's *Shorebird Ecology, Conservation and Management*, recently published by the University of California Press. I acknowledge that few persons out there run active programs in shorebird research and conservation, and that as one doing so, my students and I are the perfect target audience for the book. Anyone considering getting into shorebirds, or taking on a student interested in doing so, will want a copy, or several copies, of the book.

Whenever I take on a new student, I irrationally expect him or her to already know everything about shorebirds that I have learned over the past 40 years. Obviously, this has been a completely ridiculous assumption on my part. But in the future, I will be able to justify this expectation simply by handing the student a copy of this text and reference book for rapid education. Although our lab has had the book for only a few months, a new masters' student put it to work while developing a research proposal, and a seasoned doctoral student used it to fill some educational gaps when preparing to defend her thesis proposal. I initially used it to bolster my fuzzy memory of citations, but while going through it for this review, I was reminded of work I had nearly completely forgotten, including some of my own! The book is obviously of value for any professional considering starting a study of shorebirds or who has some managerial responsibility for their habitat.

Colwell benefits from having had personal experience with the biology of both breeding and nonbreeding shorebirds, inland, upland, and coastal systems, and having intensively studied at least one plover, a tringid, wintering calidrids and curlews, and a

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