

Penguins

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EDITED BY R. TODD ENGSTROM

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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Penguins.—Lloyd S. Davis and Martin Renner. 2003. Yale University Press, New Haven, Connecticut. 212 pp., 8 color plates, 27 data figures, 9 tables, line drawings by Sarah Wroot. ISBN 0-300-10277-1. Cloth, \$40.00.—How to make sense of penguins? Penguins are birds that forsook the air for the sea; they are highly specialized, but nonetheless occur over a wide geographic area and in exceptionally diverse habitats ranging from Antarctic to equatorial; and they comprise 16–18 species that are in some ways remarkably uniform, in other ways quite diverse.

Nearly everything about penguins, according to Lloyd S. Davis and Martin Renner in their excellent new book *Penguins*, is understandable as a consequence of the trade-offs inherent in penguins' unique double life, maintaining as they do, a foot—or flipper—in two worlds. The necessity of nesting, raising young, and molting on land but finding their food at sea explains much of the morphology, physiology, life history, and behavior of these birds that have long fascinated humans—scientists and nonscientists alike.

As the authors state in the preface, this book is not intended as a compendium of everything known about penguins. For that, a reader may be better served by Tony Williams' encyclopedic volume *The Penguins* (1995). Rather, this book calls to mind George Gaylord Simpson's 1976 classic *Penguins: Past and Present, Here and There*, which selectively treated aspects of penguin biology and evolution of particular interest.

Like Simpson, in writing a scientific book on penguins, Davis and Renner faced the unusual challenge of a subject that excites great popular interest and at the same time has proved to be

a highly productive focus of scientific research. Indeed, the authors had a more daunting task than Simpson because of the welter of scientific contributions in the fields of behavioral ecology, animal physiology, and evolutionary biology resulting from studies of penguins in the last quarter century. Nonetheless, the authors succeed admirably, producing an accessible yet scientifically rigorous monograph with a new perspective on the biology, ecology, and evolution of penguins. Readers of all backgrounds will find it useful and informative. They will also find it highly engaging, as it effectively conveys the authors' contagious fascination for penguins and the scientific conundrums they present.

The book begins with an overview of the authors' central contention of the primacy of the interplay between penguins' evolutionary legacy of terrestrial breeding and current ecological conditions penguins face in the marine environment. That is followed by eight chapters, each of which addresses a major topic in depth. Each chapter frames the topic of interest in nontechnical terms at the outset with a minimum of references, allowing the interested nonspecialist to fully grasp the ideas at play. The discussion then becomes progressively more detailed and technical, satisfying the specialist's desire for specifics and sources. With each new topic, the authors also include explanations of the methods used to obtain the information presented. That will be appreciated by all readers who are not already well acquainted with the particular research area.

The first of the subject-area chapters is a thorough treatment of the evolution of penguins, examining phylogenetic relationships among

penguin species and between the penguins and their closest non-penguin relatives. Davis and Renner bring the reader up to date on the results of diverse approaches to resolving those relationships, from comparative morphology to molecular methods, as well as more speculative evidence based on patterns of behavior and host-specificity of parasites. The authors' synthesis of those results indicates that although the precise relationships remain unsettled, penguins' closest relatives appear to be the loons, petrels, and some of the Pelecaniformes. Interestingly, although loons do not use their wings to propel themselves in the water (as penguins do), morphological evidence suggests that the ancestors of loons did. Among the more interesting conclusions regarding relationships among current penguin species is that the Magellanic Penguin (*Spheniscus magellanicus*) appears to be more closely related to the African Penguin (*S. demersus*) than to the Humboldt Penguin (*S. humboldti*), with which it shares part of its range.

The section on penguin evolution is followed by a chapter summarizing the physical characteristics, distribution, natural history, and population size of each of the current penguin species. Those species accounts are short—generally less than a page—but are detailed enough to give a good sense of the differences among species, differences the authors address in following chapters. Of particular interest in this chapter is the discussion of the disputed taxonomic status of putative species, such as the Royal (*Eudyptes schlegeli*) and White-flipped (*Eudyptula albosignata*) penguins. The authors make a case for subspecific status for both (*Eudyptes chrysolophus schlegeli* and *Eudyptula minor albosignata*, respectively), but suggest that species status may be warranted for the Northern Rockhopper Penguin (*Eudyptes chrysocome moseleyi*), currently relegated to population or subspecies status by most authorities. Although this may seem an academic dispute of little relevance, I would add emphasis to the authors' statement that these matters have great practical importance, given the threatened status of many penguin species and the profound influence taxonomic status can have on allocation of conservation resources.

Having established the evolutionary and taxonomic background, the authors spend the bulk of the book amplifying on their central premise that

the penguins' life in two worlds—and the trade-offs that result—shape all facets of their existence. Stated in its general form, that contention is perhaps obvious, albeit very effectively elaborated by the authors. What is not so obvious are the diverse, and in some cases unexpected, ramifications of those trade-offs for specific aspects of penguin breeding biology, behavior, and life history. Exploration of those ramifications is where the real strength of the book lies.

At the heart of this view is the primary importance of how far penguins must travel to find food. That factor not only influences penguins' foraging behavior and energy consumption, but will also determine the timing and duration of absence from the nest, mate, eggs, and chicks, which in turn can affect everything from timing of breeding to nest and mate selection. With those effects in mind, the authors meaningfully categorize penguins as inshore and offshore feeders, and show that many life-history parameters are correlated with distance to food. Using several well-studied examples, they describe the diversity of inshore and offshore foraging across species, as well as the diversity within species. For example, comparison of Little (Blue) Penguins (*Eudyptula minor*) at two breeding sites in New Zealand indicates that distance to food has large effects on virtually all aspects of breeding, from timing to success.

As the authors say, such variability in breeding behavior in a single species in response to differences in prey availability, along with diet studies showing that single species of penguins exploit diverse prey, indicates a high degree of flexibility in penguins, at least in their foraging ecology. It also suggests a resolution to the apparent paradox of penguin uniformity and diversity: morphological similarity of species may be explained by the uniform hydrodynamic constraints imposed by aquatic movement, whereas the diversity of behaviors and foraging patterns across species reflect more variable ecological conditions, such as prey distribution.

After convincingly establishing the flexibility of penguin foraging, Davis and Renner go on to contend that penguins, being dietary generalists, do not partition food resources among species. That conclusion may be premature. Although the authors present some evidence to support the claim, they also include a counter example; and results of a recent study (Boersma

et al. 2002) indicate that three penguin species breeding simultaneously at one location forage in different areas.

In successive chapters, the authors treat topics of breeding-site selection, mate selection, parental investment, and molt and migration, all interpreted in light of the importance of foraging distance and the trade-off between terrestrial breeding and aquatic foraging. For example, the authors make the point that offshore breeders tend to be older at first breeding than inshore feeders, which suggests that they must develop greater foraging efficiency before breeding. They also observe a negative correlation between species' average foraging distance and likelihood of raising two chicks, and show that because of differences in the pattern of parents' return to the nest, the greatest risk of chick starvation occurs far later for inshore-feeding species than for offshore feeders.

Along the way, the authors offer thought-provoking speculations on a variety of penguin puzzles, such as the function of chick creching and feeding chases, why crested penguins lay two eggs but raise only one chick, and why the ecologically similar penguins and auks have arrived at very different solutions to the problem of locomotion.

All of this is fascinating, and I found very little in the book to dislike. I would like to have seen the chapter on breeding site expanded to provide a more complete discussion of density, site fidelity, and coloniality, and I'm also not sure that the algebraic expression of predicted foraging distance (Chapter 4) adds to the verbal explanation of that issue. But those are minor matters of preference rather than real criticisms.

Unlike penguins, which manage to live at the margins of two worlds, we humans have occupied nearly all parts of *all* worlds, leaving little room for the other inhabitants of the planet. Appropriately, the book ends with a comprehensive review of research related to conservation of penguins. Again, the distinction between inshore and offshore foragers is relevant, because inshore species, dependent on reliable and local food resources, are generally more seriously imperiled. Like many organisms, penguins are vulnerable to threats of habitat loss, invasive species, and exploitation; and the authors' review of recent work directed at understanding and addressing those threats gives reason for some encouragement. On the other hand, the status of

many penguin species is tenuous, and Davis and Renner identify serious threats to penguins that remain poorly understood and need more study. Among those are the effect of commercial fish harvest on food availability, climate change, and biomagnifying of toxic pollutants. In addition, given penguins' popular appeal, their potential as ambassadors for marine conservation, and the growth of international ecotourism, the effects of human disturbance on penguins must be better understood. In light of the diverse and subtle disturbance effects summarized by the authors, investigation of that topic should be incorporated into nearly all field studies of penguins, with both significant and nonsignificant effects reported.

Finally, the brevity of the section on penguin migration indicates a great need for more work on that topic. Our understanding of penguin foraging ecology, though still incomplete, has advanced substantially, as indicated by the appearance of this book, which could not have been written even five years ago because of the paucity of information that existed then on the at-sea lives of penguins. We are now similarly limited in our knowledge of penguin migratory behavior, which will be essential for developing the large-scale measures necessary to effectively conserve the many migratory species in this group.

In summary, this is a valuable contribution to the expanding literature on the biology of penguins. It presents a new and important perspective and is engagingly written, thoroughly researched, and attractive to look at, with excellent color and black-and-white photographs as well as interesting and illustrative drawings. Both scientifically rigorous and exceptionally readable, this book will appeal to all those who study penguins, and many who simply love them.—DAVID STOKES, *Department of Environmental Studies and Planning, Sonoma State University, Rohnert Park, California 94928, USA. E-mail: stokes@sonoma.edu*

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The Speciation and Biogeography of Birds.—Ian Newton. 2003. Academic Press, Amsterdam. xii + 668 pp. ISBN 0-12-517375-X. Cloth, \$75.00.—Thanks to advances in phylogenetic methods and molecular systematics, the fields of speciation and biogeography have advanced at a tremendous pace. For a researcher entering this field, the literature presents a formidable challenge, and a synthesis of research in biogeography and speciation has been sorely needed. Ian Newton's book, *The Speciation and Biogeography of Birds*, is an awkward step in this direction. Part of the awkwardness comes from confusion as to what the book is actually about. The book traverses a large number of issues, from the role of humans in causing extinctions, productivity of marine environments, dry-wet cycles, glaciation, ecological issues (habitat, food, predators, parasites, competition), and migration, to the molecular clock, to mention a few. After reading the book, it is clear that it is not about speciation or historical biogeography; instead, it is a book about ecological biogeography. The lasting contribution of the book is in its summary of avian distributions and natural history, not in the phylogenetic interpretation of speciation and biogeography.

The fields of speciation and biogeography are inherently rooted in phylogenetic reasoning. However, this is not Newton's main area of expertise, which renders some of the sections in Part 1, which focus on "Evolution and Diversity of Birds" misleading. In particular, the sections are grounded in the school of "evolutionary systematics" (e.g. Mayr and Ashlock 1990), which is not the paradigm used by the majority of modern systematists. Thus, we cannot recommend those sections as a general introduction for a student of ornithology or evolution. Newton prefers the Biological Species Concept for its "recognition" of varying levels of diversity, such as superspecies, subspecies, and allopecies. Newton views those taxonomic categories as objective and uses them as a basis

for his analyses. However, the monophyly of few of those taxa have been corroborated by phylogenetic analysis, rendering them potentially inappropriate for his intended use. Newton notes that morphological assessments of evolutionary relationships can be compromised by convergence and that DNA characters are potentially more objective. Convergence is indeed a problem with morphological data, but phylogenetic (cladistic) methods are much better able to detect it than the evolutionary systematics that Newton favors. However, Newton also states that molecular phylogenies and molecular clocks might not be trusted because of many untested assumptions. Although certainly true in some cases, it is the morphological assessments—mostly subjective, non-character-based, and precladistic—that are equally, if not more, suspect. Thus, strengths and weaknesses of different types of data and methods of phylogeny reconstruction are not clearly presented. Perhaps not surprisingly, in the entire book, there are only three phylogenetic trees, the most recent of which was published in 1996.

There are several other problems with the treatment of molecular systematics. Newton equates taxonomic rank with genetic distance rather than tree topology. He states that DNA–DNA hybridization is important for "resolution of the older branches" in the avian tree; however, we know of no lab that still uses DNA–DNA hybridization for phylogenetic inference, because it is recognized that sequence analysis is preferable for all depths in the avian tree of life. Newton repeats (p. 500) the common misperception in the literature that microsatellites evolve more rapidly than mtDNA because of a higher mutation rate. It is indeed a result of Kimura's neutral theory that for strictly neutral traits, the fixation rate equals the mutation rate, independent of the population size. However, this is for loci in the same genome. The confusion stems from misunderstanding of "evolve more rapidly." Although some microsatellite loci have high mutation rates and hence many alleles, it does not follow that those loci have a better chance of capturing population isolation than an mtDNA gene tree. The nuclear genome, because of its mode of inheritance, coalesces on average of four times more slowly than does the mtDNA genome.

Several other problems are worth noting. In comparing the number of species in sister clades, Newton states (p. 350) that the clade