The Flexible Phenotype: A Body-Centred Integration of Ecology, Physiology, and Behavior

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The Flexible Phenotype: A Body-Centred Integration of Ecology, Physiology, and Behavior.—Theunis Piersma and Jan A. van Gils. 2011. Oxford University Press, Oxford, UK. 256 pp. ISBN 978-0-19-959724-6. $52.95 (paperback).

Scientists write books for a variety of reasons, including to garner some freedom from the too often suffocating world of journal editors and peer reviewers, although there are some equally pugnacious book editors. Writing scientific books provides us a chance to summarize science from a personal perspective, to present ideas in a liberating manner, to reach audiences who rarely venture to our favorite scientific journals, and, in the best of cases, to integrate established ideas in creative and unifying ways that provide new insights. Piersma and van Gils have successfully accomplished this in their impressively well-written new book *The Flexible Phenotype*.

These two outstanding Dutch scientists have written a book that champions the perspective and studies of Dutch evolutionary ecologists. As they note in the final chapter of the book, they foster the views that "organisms and their particular environments are inseparable" and "phenotype–environment interactions need to be studied functionally" (p. 174). The authors draw heavily from their own ground-breaking studies of the Red Knot (*Calidris canutus*) and other shorebirds, as well as the original work of Rudi Drent (to whom the book is dedicated), Serge Daan, Nikko Tinbergen, and the many other animal ecologists associated with University of Groningen (the list is long and illustrious). This perspective of animal ecology includes, as the subtitle of the book implies, an integrated view of animal physiology, behavior, and evolution.

Consistent with this Dutch perspective, the vast majority of the original figures in the book were produced in collaboration with Dick Visser, whose creativity, graphic talent, and unique style enhance the value of the work immensely. Any of us who have read even a few of the hundreds of animal ecology papers produced by students and faculty from the University of Groningen can appreciate Dick Visser's stamp on the figures. The ideas described in the text are illustrated regularly and to great effect throughout the book. The figures alone are worth the purchase price.

While we were reviewing the book, a plant ecologist colleague noticed it on our desk and was quite excited by the title since her work addresses the importance of plants' flexible phenotypes given certain genotypes and the evolution of invasiveness. But this is not such a book even though the concept of phenotypic flexibility is so broad. Instead, this is a book mostly about flexible phenotypes of vertebrate animals, about how the behavior, physiology, and morphology of animals respond to environmental variability and predictability. The majority of examples are from birds, especially the Red Knot, but there are enough examples from other critters (barnacles and *Daphnia* to astronauts and cosmonauts) to satisfy many animal ecologists.

The book begins with a brief introductory chapter that describes the main characters (migratory birds, in general, but usually Red Knots), the general perspective of the authors (integrative biologists who view the behavior, physiology, and behavior of organisms within an ecological and life-history context; see their Fig. 1), and the rationale for the authors' choice of content and organization of the book. The next two chapters (Part I) introduce "rules of organismal design," including a basic introduction to animal energetics and nutrition, heat and water balance, and how these relate to functional capacity, spare capacity and symmorphosis, and allometry. These short reviews are well organized and succinct yet often lack discussion of alternative hypotheses and criticisms of some of these basic concepts.

In Parts II and III, the authors explicitly relate the physiology of animals (Part I) to their environment, and both how (proximate) and why (ultimate) this creates limits (metabolic ceilings) to animal performance. These chapters provide good reviews of phenotypic plasticity in morphology and physiology (Chapter 5) as well as behavior (Chapters 6, 7). The authors provide a useful summary of the various types of phenotypic plasticity and a taxonomy of sorts for characterizing how environmental predictability and variability are related to different types of plasticity in physiology, morphology, and behavior. As promised, each of these general concepts is simply but adequately described, and then usually studies of the Red Knot (the "empirical backbone" of the book) are used to illustrate these concepts (exclusively so in Chapter 7). However, Chapters 5 and 6 include examples of how a variety of animals change their morphology and physiology (i.e., their phenotype) during ontogeny, across seasons, during their life-cycle stages, and in direct response to environmental conditions. The book to this point provides the introduction that the authors deem necessary for a more fully integrated view of flexible phenotypes to be understood and appreciated (Part IV).

The last three chapters, which constitute Part IV, provide a review of how studies of the Red Knot have enlightened our understanding of the functional significance of phenotypic flexibility: examples include body-composition change in relation to predation risk and migration strategy in relation to disease risk and investment in the immune system. These studies are impressive in their breadth and depth, although this myopic focus on one species neglects other important work that would enable a more complete consideration of alternative hypotheses in relation to the evidence. The chapter on disease risk and the immune system is full of ideas unrestricted by empirical data and in sore need of testing. Chapter 9 highlights the applied aspects of these types of studies and the important implications of phenotypic flexibility for the conservation of our study species. The final chapter acknowledges the work of others in the development of Piersma and van Gils' perspective on the importance of both genetic and epigenetic inheritance in evolution and the central role of phenotypic variation and the flexible phenotype in how the actors (our beloved animals) are influenced by the theater (the environment) and vice versa.

We always expect from a good book review some complaints or at least an enthusiastic critique, given that

nothing is perfect except perhaps young love, Bavarian beer, and the wonders of nature. Tradeoffs are intrinsic to any enterprise including life history as well as writing books from a personal perspective—they provide originality and insights, if done well, but they are always fraught with intrinsic bias. Thus, one concern with this book is that at times the perspective of these two Dutch scientists is rather parochial and lacks acknowledgment of some key contributors. For example, there are many important studies of the ecology of the Red Knot during its migration through Delaware Bay (a key stopover site in eastern North America), yet surprisingly few of these studies are cited in this book. There are also several key concepts (e.g., flexibility of digestive system) that the authors use as prime examples of how the environment influences animal physiology (and so this topic is placed in the "matching phenotypes to environmental demands" section of the book), even though there is a rich literature on how this flexibility is responsible for physiological constraints that in turn have important ecological implications (we would have emphasized this topic in the earlier section on "physiological constraints"). We grew less and less concerned about the authors' perspective as we read further—in short, we recognized this perspective, we will rely on other sources for more complete reviews of key topics and controversies, and we will continue to come back to this book for nice summaries of many key topics, and for original synthetic, well-illustrated ideas.

Another concern of note is that the authors assume that the book is read from cover to cover, as there are many references in later chapters to earlier examples and concepts. This may limit the flexibility provided in other texts that are organized as more stand-alone chapters and topics. Since we both read the book from cover to cover, we were not so distracted. However, we strongly recommend that all readers read the book from the first to the last page to maximize their understanding and enjoyment of this fine book. Last, the Red Knot is a classic example of many of the key concepts covered in this book. However, at times the connection to this exemplary shorebird seemed strained and the point could have been better illustrated with studies of other animals. This last criticism will be immaterial to ornithologists, especially those who study shorebirds, who will really like the shorebird bias, but those who study other critters may feel less accommodating.

In general, this book achieves the goal of the authors in providing a succinct state-of-the-art review on phenotypic flexibility of animals. It should be of interest to a broad range of scientists interested in physiology, behavioral ecology, and evolutionary biology and who study most any animal. Graduate students and researchers interested in updating their knowledge of physiological ecology and phenotypic flexibility of animals will be well served by this book. The figures and other illustrations are outstanding and will enhance many a lecture and find homes on many refrigerator doors and lab walls. The book deserves a spot on your bookshelf next to other fine volumes on animal physiology and ecology.—SCOTT R. McWILLIAMS, Program in Wildlife & Conservation Biology, Department of Natural Resources Science, University of Rhode Island, Kingston, RI 02881; E-mail: srmcwilliams@uri.edu, and ULF BAUCHINGER, European Research and Project Office GmbH, Science Park 1, Stuhlsatzenhausweg 69, 66123 Saarbrücken, Germany; E-mail: u.bauchinger@eurice.eu.