

Sex, Size & Gender Roles: Evolutionary Studies of Sexual Size Dimorphism.

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BOOK REVIEWS

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Sex, Size & Gender Roles: Evolutionary Studies of Sexual Size Dimorphism.—Daphne J. Fairbairn, Wolf U. Blanckenhorn, and Tamás Székely, editors. 2007 (paperback 2009). Oxford University Press, New York. 280 pp. ISBN-13: 978-0-19-954558-2. \$60.00 (paperback).

Sexual dimorphism is widespread among animals and plants and has attracted the attention of biologists for decades. This volume edited by Fairbairn, Blanckenhorn, and Székely assembles current research on the many fascinating, yet puzzling, patterns of sexual size dimorphism in animals and beyond. Indeed, Chapter 1 by Fairbairn is a great overview of why sexual dimorphism is such an interesting topic to evolutionary biologists, why it is paradoxical, and why it can be difficult to study empirically. The remainder of the volume is divided into three sections, each covering a different approach to the study of sexual dimorphism in size. The first two sections address the adaptive significance of sexual size dimorphism by examining its broad-scale patterns across taxa (Section I) and testing specific hypotheses about its adaptive value within a species or among closely related species (Section II). The final section (Section III) leaves the realm of adaptive significance and deals with the proximate genetic and developmental mechanisms that lead to sexual differences in body size. Although the topics in the first two sections overlap somewhat, the three sections do a remarkable job of representing the diversity of approaches that evolutionary biologists take when studying the evolution of sexual size dimorphism. The three sections are each well integrated by an introduction, each written by a different editor, and the introductions admirably summarize and synthesize the salient points of each chapter.

Section I has six chapters detailing large-scale patterns of sexual size dimorphism within several major animal groups. Although there is a vertebrate bias to this section (only two of the six chapters deal with invertebrates), it represents the state of current knowledge and should serve to catalyze future research on sexual size dimorphism in invertebrates, which display some of the most fascinating and extreme patterns of dimorphism. Most chapters present tests of whether sexual selection, rather than other factors, drives the evolution and maintenance of sexual size dimorphism. Most also test Rensch's Rule within the group of interest. Rensch's Rule is a common pattern in which sexual size dimorphism increases with body size in taxa where the male is larger but decreases with body size in taxa where the female is larger. The differences among taxa in patterns of sexual size dimorphism, as summarized in this book, are striking and serve as a good reminder that what we study in our own focal species, or group of species, may not be the norm in other species. Rensch's Rule is generally supported, largely because of sexual selection on males, in most vertebrates studied (mammals: Chapter 2, Lindénfors et al.; birds: Chapter 3, Székely et al.; reptiles: Chapter 4, Cox et al.). Because of a general lack of data on dimorphism in

amphibians, however, it is unclear whether this pattern exists in that class (Chapter 5, Kupfer). Because birds have been the focus of numerous field studies, and phylogenies are available for comparative analyses, they represent a good group for testing specific adaptive hypotheses concerning the evolution of sexual size dimorphism (Chapter 3, Székely et al.). In birds, most frequently it is the male that is larger, and the authors conclude that mating competition and males' agility have contributed significantly to the patterns of sexual size dimorphism that we see today, though these hypotheses do not explain all of the observed variation. Their analyses across a wide range of species demonstrate the power of broad-scale tests, but they also highlight the lack of precise quantitative data for many relevant aspects of many species' phenotype. For example, Székely et al. tested the male-agility hypothesis, which posits that competition between males favors smaller individuals that have the advantage of increased maneuverability or agility. This hypothesis likely explains males' small body size in many birds and has good potential to explain why males are the smaller sex in many species of gliding and flying animals despite the influence of strong sexual selection. In the analysis of Székely et al. "agility" is necessarily a coarse categorization, not a quantity measured in actual flight performance. This lack of data is a good reminder of work that still needs to be done in the quest to explain patterns of dimorphism.

The invertebrates studied seem to show patterns of sexual size dimorphism that are different from most vertebrates. Chapter 6 (Blanckenhorn et al.) describes patterns in insects, an extremely diverse group in which the female is generally larger. In contrast to most vertebrate groups, the authors found little support for Rensch's Rule across species or within species. They suggest that variation in females' size, rather than males' size, has contributed more to patterns of dimorphism, a finding counter to Rensch's Rule. In Chapter 7, Foellmer and Moya-Laraño reached the same conclusion for spiders, a group that covers the whole continuum from male larger to female larger and has perhaps the most striking examples of dimorphism (some with sexual differences in mass of over two orders of magnitude!). The diversity of findings across these six chapters, as well as the remaining ambiguities in what factors explain sexual size dimorphism in each group, promise to keep evolutionary biologists busy for many years to come. With key data still missing for thousands of species in each group, the results of future comparative studies that take new data into account will be exciting to see.

Section II contains eight chapters that take more fine-grained approaches to the study of sexual size dimorphism within a species or among closely related species. Because insects are amenable to microevolutionary studies of selection, invertebrates are represented better in this section. Many of these chapters attempt to answer what specific advantages being small or large has for fitness. That is, does selection differ by sex, and,

if so, how do we detect the difference? It is often presumed that for sexual size dimorphism to be maintained over evolutionary time males and females should experience different selective pressures, but this assumption has proven difficult to test. Chapter 8 (Fox et al.) synthesizes work on two species of seed beetles with opposite patterns of sexual size dimorphism. In species in which the male is larger, males experience fecundity selection to produce larger nuptial gifts for females, but this selection is absent in species in which the female is larger. Chapter 9 (Fairbairn) synthesizes work on sexual size dimorphism in water striders. The strength of this chapter is the quantification of selection on each sex at various ontogenetic stages and for multiple traits. Males and females both experience opposing selection on body size, resulting in net stabilizing selection. Considering ontogenetic and sexual differences in selection on the same traits has great promise for future studies. Chapter 10 (Blanckenhorn) takes a similar approach, investigating selection in two species of dung flies that have opposite patterns of dimorphism. The finding of both sexual selection and fecundity selection for large size in males, but no opposing selection, does not support the hypothesis that the equilibrium of opposing selective forces in the two sexes differs and points to constraints that may explain the observed patterns. Chapter 11 (Delph) is the single contribution in this book that discusses dimorphism in a plant. Combining experimental data and studies of artificial selection reveals that in males selection on flower number has a suite of effects on genetically correlated traits, a phenomenon that is likely widespread in many taxa, including animals. Chapter 12 (Capellini) discusses work on the species of hartebeest (*Alcelaphus*) to describe what is often presumed to be the typical balance between natural and sexual selection in explaining males' investment in secondary sexual structures, in this case horns. Chapter 13 (Kalmbach and Benito) presents a comparative analysis of mortality of offspring in birds to explore whether dimorphism in adulthood can be explained by selection at earlier stages of development. Their analysis of sexual size dimorphism and nestlings' vulnerability across species suggests that the sex that ultimately ends up the larger pays a cost in viability and that this disadvantage is exacerbated for the male.

Chapter 14 (Roitberg) examines variation in sexual size dimorphism across seven subspecies (among 52 populations) of the widespread lizard *Lacerta agilis*. Although differences in sexual selection pressures on males likely explain some of the observed variation in dimorphism, climate has also likely played a role in shaping the body size of both males and females. Chapter 15 (Kratovichil and Frynta) is a comparative study of sexual size dimorphism in several species of eyelid geckoes. Their phylogenetic approach was necessary to show that combat between males is evolutionarily associated with dimorphism in which the male is larger but that courtship complexity and relative egg size are not associated with a shift to dimorphism in which the female is larger. This chapter is a reminder that dimorphism in a species often did not evolve *de novo* but instead was inherited from an ancestor. This realization can change the focus of research questions and how they are answered. The strength of Section II is that it encourages readers that one can actually test whether the sexes differ in selection pressure on body size (and/or other body features) and determine what factors cause those differences. Methods described in this section can be used by biologists studying a wide variety of taxa. It would have been nice if a bit more attention had been paid to dimorphism in shape or how we should study the evolution of body proportions. However, this is a book about body size specifically, so I hope a future volume will deal strictly with issues of allometry and shape.

Section III consists of five chapters that deal with proximate factors contributing to sexual size dimorphism. Chapter 16 (Rhen) takes a phylogenetic approach to the extreme by looking back to the divergence of living organisms into the currently recognized domains of life. Looking so far back reveals that sexual differences have arisen twice among eukaryotes (in plants and in animals), but are essentially nonexistent in the remaining eukaryotes (fungi and protists) and in prokaryotes. This chapter, as well as the next two, emphasizes the difficulties in understanding how males and females can differ so markedly when they are constrained by sharing the same genome. Rhen summarizes several potential proximate mechanisms that may result in sexual dimorphism, including sex linkage, sex-limited expression of autosomal loci, phenotypic plasticity, and genomic imprinting. The latter mechanism, in which the offspring expresses alleles from its mother and father differently, is explored in more detail in Chapter 17 (Bonduriansky). Recent technological advances will allow further testing of this chapter's hypotheses that predict differences between the sexes in silencing of parental alleles according to the alleles' effects on fitness. Bonduriansky also emphasizes how allocation of resources toward secondary sexual traits and viability (i.e., condition dependence) is underappreciated in studies of sexual size dimorphism, though this topic is being addressed increasingly. Chapter 18 (Bedhomme and Chipindale) reviews how sexual conflict, especially intralocus sexual conflict, may be resolved. It suggests that intralocus sexual conflict may be widespread and contribute to maintaining genetic variation in populations but it emphasizes the difficulties of detecting this phenomenon since what we currently see is at least partial resolution of such conflict. Chapter 19 (John-Alder and Cox) reviews work showing how the steroid hormone testosterone can either promote or inhibit growth of male lizards, depending on whether the male is the larger or smaller sex in the species. Such a mechanism is intriguing, and it will prove interesting to see whether their finding of testosterone as a bipotential growth regulator applies also to other vertebrates. Indeed, because the exact manner in which opposite growth patterns can result from the same general hormonal mechanism is still unknown, this topic will remain an intriguing line of research. Chapter 20 (Jarošík and Honek) shows that among insects males tend to develop faster than females and that this trend is stronger in species without a true pupal stage. This pattern again stresses the importance of considering ontogenetic differences in selection as a contributor to adult dimorphism. As a more field-oriented biologist, I found this section especially interesting, and it made me wonder how such approaches would help answer some of my own research questions. I hope that readers of this book who are field biologists seek out collaborations with colleagues who use techniques discussed in Section III, as such integration holds great promise for our understanding of how organisms evolve.

What stood out to me most while I was reading this book was how each chapter is a stand-alone contribution of high quality. Furthermore, each chapter is approximately the length of a journal article, making each topic accessible to readers in a succinct fashion. Despite the independence of each chapter, all of the contributions complement each other well and emphasize the diversity of patterns of sexual size dimorphism among animals. Although many chapters support the long-held notion that sexual selection on males explains much of the variation by species in sexual size dimorphism, this book provides plenty of examples that suggest selection on female body size, and other factors, can be just as important in shaping the phenotypes that we see today. It is difficult to point to weaknesses of the volume as a whole, but one could argue that there are some minor ones. For example,

coverage of fishes is conspicuously missing, somewhat surprising given the available work on cichlid and poeciliid fishes. One could nitpick the placement of certain chapters in a given section of the book, but in general the volume is cohesive and flows well. Neither of these issues detracts from the quality of the book. Indeed, the breadth of taxa and topics covered in this volume will make it an indispensable reference for those interested in sexual dimorphism. Although there are not many chapters specifically devoted to birds, ornithologists will find the diversity of hypotheses and approaches informative and stimulating to their own research questions. This book will be of interest to ecologists and evolutionary biologists in general who study vertebrates because the numerous contributions are great syntheses of the existing literature. Yet it will also be of interest to those who study invertebrates because it highlights gaps in our knowledge of these diverse lineages. Thus, no matter what group of organisms you happen to study, this contribution does a good job of summarizing what has been done and what remains to be done to understand the evolution of sexual size dimorphism. This compilation will be especially helpful as technology continues to improve, as emphasized in Section III. Biologists have been studying patterns of sexual size dimorphism, and the evolutionary forces contributing to them, for a long time, yet we still barely understand, theoretically or empirically, many of the basic developmental and genetic factors that allow similar genomes to result in two sexes that can be so remarkably different.—JERRY F. HUSAK, Department of Biology, University of South Dakota, Vermillion, SD 57069. E-mail: jerry.husak@usd.edu.