

WHY ARE THE SEXES AS THEY ARE? MANY DATA, SOME PATTERNS, AND MANY UNSOLVED MYSTERIES¹

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Recently, in all seriousness, I was asked if the sexes were different. I answered that I thought so. “But, on what evidence?” continued my inquisitor. I replied that my favorite came from the many studies showing that parents adaptively modify the sex ratios of their progeny, so even if you do not recognize sex differences, in a huge variety of species, parents respond—or their parents’ proxy through natural selection responds—to differences between the sexes. More evidence of sex differences is in this collection of papers,¹ which explores more thoroughly than any previous book the distribution and adaptive significance of sexual size dimorphism (SSD), one of the most easily recognized forms of sex difference.

SSD is about within-population differences in the sizes of females and males. The first part—the heart of the book—is about macroevolutionary patterns comprised of six taxonomic chapters that remind us who is larger; the second part contains microevolutionary studies, whose authors seek to understand the selective pressures favoring SSD, and the last is about mechanisms of sexual dimorphism. Many data inform the description of macroevolutionary patterns, though a few obvious groups need more work and the fish were notably absent. There is an obvious need for more microevolutionary studies of SSD like those in the second

part of the book, and it is clear that those who simultaneously attempt both proximate and ultimate analyses of SSD will be rewarded.

For most species on the Earth with SSD, females are larger than males, but in those taxa most familiar to most of us, birds and mammals, males are most often larger than females. For all of mammals, the average dimorphism represented as the size dimorphism index ($[\text{mass of the larger sex} - \text{mass of the smaller sex}] - 1$, with the sign negative when males are larger and positive when females are larger) is -0.176 , nowhere near the extremes of SSD found in spiders, for example. Birds are dimorphic, usually, but not always, with males larger. Herps are more variable than mammals and birds, with both female and male biased SSD occurring in lizards (more male-biased), snakes (more female-biased), turtles (more female-biased), and crocodylians (more male-biased). In insects and spiders, females are most often larger than males. Why these Class differences matter is still opaque.

The patterns in the first part of the book contain more than mean differences between the sexes. They also contain data on the amount of variation between related taxa, and interest in this variation is captured relative to Rensch’s Rule, which states that SSD increases with size when males are the larger sex, but decreases with size when females are the larger sex. By agreement, evidence of Rensch’s Rule is found in a slope greater than one in logarithmic plots of male against female size across species. Rensch’s Rule was sometimes met in mammals, birds, herps, but was absent in insects and spiders. Given that so much space was

¹*Sex, Size & Gender Roles: Evolutionary Studies of Sexual Size Dimorphism*. Edited by: Daphne J. Fairbairn, Wolf U. Blanckenhorn, and Tamás Székely. 2007. Oxford University Press: Oxford and New York. 266 pp. HB \$110.00, ISBN 978-0-19-920878-4. I thank S. P. Hubbell for useful comments on a previous version.

given over to Rensch's Rule, and given that so much of the data were equivocal—often data fit expectations, but often they did not, and sometimes data rejected the rule (insects and spiders)—it was difficult for me to garner what remains of the rule in Rensch's Rule. Furthermore, my ability to read German is primitive, so I did not read Rensch's original paper, and I wonder what he thought his "rule" meant. Whatever it might mean, based on the data in this wonderful book, it would seem reasonable to demote Rensch's Rule to Rensch's Hypothesis.

Most chapters considered or at least gave a nod to four functional hypotheses explaining variation in SSD: sexual selection (males expected to be larger, when male–male combat or other male contests over access to females are common), display agility (another explanation based on male–male sexual selection, but with males expected to be smaller than females to facilitate rapid or fancy movements or the ability to find females), resource partitioning (the larger sex exploiting larger prey or food items), and fecundity selection (larger females favored by larger clutch or brood sizes). Most evidence to date seems to favor sexual selection acting through male–male combat. However, the database even for these conclusions is weak in that in most of these tests, the presence of sexual selection acting on males was inferred because males fight. The data that would allow tight associations between sexual selection acting through male–male competition over number of mates are absent for most species, and the tests for effects of fecundity variation on female size—within populations—are almost entirely lacking, so this hypothesis too can only be subjected to weak tests. The hypothesis that variation in SSD is favored by sexual conflict (meaning male attempts to control female reproductive decisions and female attempts to resist others' control) was mentioned a few times, but not systematically tested in any of the chapters, which is the only complaint I have about this big, pithy book. Clearly, despite all that is known, there is more to do. Graduate students should take note.

For those who wonder how to proceed, the middle sections of the book give examples. There are two main ways: either do a study of within-population individual variation in lifetime fitness and body size (thereby capturing the costs and benefits of body size variation) or do a cross-sectional study of between-individual, within-population variation. The most impressive of the studies in this section include ones by Daphne J. Fairbairn, on water striders, *Aquarius remigisan*, and by Wolf U. Blanck-

horn on two species of dung flies, *Scathophaga stercoraria* and *Sepsis cynipsea*. Fairbairn rejected the hypothesis that SSD was adaptive during nymphal stages and the hypothesis that SSD was due to sexual bimaturism and differential selection on development time. She found little evidence for ecological divergences between the sexes prior to the onset of reproductive activity, and although overwinter survival is associated with lipid reserves and eclosion dates, neither differed between females and males. She did not look at the effects of female size and their ability to dislodge some males, so in the system with overt phenotypic sexual conflict there appears to be no test of the hypothesis that female size variation is associated with variation in offspring quality. To me this part of the book was the guts, as it had data reliable for conclusions about within species SSD, where hypotheses of functional significance must be tested. These are the chapters students should read and think about most carefully for these are the path-breakers among all the chapters in the book.

The next time I am asked about whether the sexes differ, I will refer my inquisitors to this book that contains more than most will want to know about the evolution, development, and proximate control of phenotypic differences in the sexes. For those of us professionally interested in sex differences and their origins, the book is full of data, analyses, and ideas. What I really like about it though, is that it makes clear that there is so much more to do. It will be the citation classic of the future for pointing the way. For example, what we think we know about the adaptive significance of sex differences is subject to significant debate. Our hypotheses need refinement—even given the considerable elegance of many of the author's chapters and particularly the chapters by each of the three editors. Our hypotheses seem very facile, simultaneously able to explain bigger and smaller males using the same hypothesis of sexual selection, yet also spare, only able to explain big females via fecundity selection. Despite all the hard work of all these authors and the three insightful editors, what we know about "sex specific selection" remains small, so some of the most exciting work is in the future, making it likely that my prediction that this collected volume will be a citation classic a very good bet. It is this promise and pithiness that made me admire and savor this book and brings me to recommend it as an ideal focus for graduate seminars.

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