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Sexual Selections: What We Can and Can't Learn about Sex from Animals

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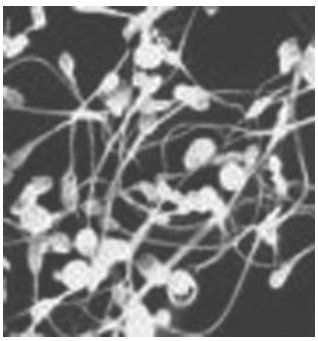
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What We Can and Can't Learn about Biology from Feminism

Sexual Selections: What We Can and Can't Learn about Sex from Animals. Marlene Zuk. University of California Press, Berkeley, 2003. 250 pp. $16.95 (ISBN 0520240758 paper).

The temptation to infer humanlike motivations and thought processes can be hard to resist when watching animals engage in behaviors with seemingly obvious human parallels, such as a courtship rituals. Anthropomorphism, however, can lead to flawed interpretations of animal behavior, particularly when combined with sexist biases and stereotypes. Marlene Zuk, a professor of biology at the University of California, Riverside, argues these points in an engaging, highly readable, and thought-provoking book, *Sexual Selections: What We Can and Can't Learn about Sex from Animals,* now available in paperback. The pitfalls of anthropomorphism are illustrated to great effect with a number of entertaining examples, many of which document a distinct male bias. Zuk argues that feminism can provide anthropomorphist biologists with the intellectual tools needed to cure their bad habits.

In this lively and humorous book, Zuk skillfully highlights the often-missed tendency in biology to view interactions between the sexes from a male perspective. This has led some to the absurd notion that female reproductive concerns are unimportant, or at least uninteresting.



Zuk's book was written to draw attention to this bias, and here the book is at its best, packed with examples of observations by biologists of behavior that challenge sexual stereotypes. This abundance of examples, unfortunately, does rather undercut the other axis of this book—the suggestion that feminism is needed to correct the bias—since many of the contrary observations were made by scientists without an explicitly feminist agenda.

Zuk repeatedly asserts that "feminism has more to offer biology than vice versa," but the book is not completely persuasive in this respect. It is indeed important, as Zuk suggests, to be "aware of the stereotypes to be able to break them." Ways of thinking honed by feminists experienced at detecting bias in society at large may be helpful for detecting bias in science. But feminism is an ideology and consequently incorporates not just ways of thinking about problems but also beliefs and biases of its own. So even if, as Zuk suggests, researchers have too often in the past been constrained and biased by male chauvinism, is feminism necessarily the best remedy? Is offsetting one bias with another an aid to objectivity? Zuk showcases the work of many scientists who, like herself, are feminists, but their work is excellent not because they are good feminists but because they are good scientists. Feminism may have helped throw male bias into sharp relief, but biology provided the tools to rectify it.

As for the claim that male chauvinism has hampered progress in biology, some of Zuk's examples are convincing, but others are less so. For example, in chapter 5, "The Care and Management of Sperm," Zuk examines how research on sperm competition has tended to focus on male adaptations, such as the ability to allocate sperm prudently, rather than female adaptations that might influence the outcome of such postcopulatory competition. In many species, sperm do not seem to survive in the vagina as well as might be expected if sexual reproduction were an entirely harmonious and cooperative venture. Consequently, some researchers have described the vagina as a "hostile" environment for sperm. Zuk finds this troublesome, and suggests that while it may seem "hostile" from a male perspective, it could equally be described as "selective." This is not, however, simply a matter of terminology and perspective. "Hostility" can be readily and directly observed, for example, if sperm die more quickly when suspended in vaginal fluid, rather than just seminal fluid. So the vaginal environment may be objectively hostile to sperm, but to describe it as "selective" presumes a function and implies that sperm mortality may be nonrandom with respect to an individual sperm's haplotype or to the male partner's diploid genotype. Selectivity there may very well be, but that is an empirical question that follows from the initial observation of "hostility."

It is true that not a great deal is known about what happens to sperm inside a female, but the reasons for this, as for many other examples of apparently neglected topics in biology, are probably methodological rather than ideological. It is simply a lot easier to study sperm emitted by, or extracted from, a male than it is to study interactions between, and active manipulation of, sperm within the female reproductive tract. This is most likely why direct evidence of postcopulatory sperm selection by females is scarce across species, and the exceptions tend to emphasize this point. It has been shown that female feral fowl actively eject sperm from lower-ranking males (Pizzari and Birkhead 2000), and there has been some work on the functional significance of the human female orgasm (discussed in chapter 9, "Soccer, Adaptation, and Orgasms"). Not coincidentally, both these phenomena have been studied using as a source of data sperm ejected from females. Sperm are more amenable to study when they are not hidden in ducts and crypts. Some insights into how females

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might control sperm usage within their reproductive tracts have been obtained by rapidly freezing insects *in copula* (Hosken and Ward 2000), but such a chilling form of coitus interruptus is obviously not appropriate for all species.

Other supposed examples of male bias may also stem from practicality rather than chauvinism. As Zuk points out, technological innovations such as DNA haplotyping have yielded findings that have challenged the prevailing view that promiscuity is beneficial only for males. This notion grew largely out of observational studies of mating behavior, usually a more important determinant of fitness for males than for females. This does not imply that female behavior is unimportant, but merely that it is more convenient to study overt behavior by males than covert paternity allocation inside females. Developments in methodology have provided the evidence that females do have something to gain from mating with multiple males. For example, there are possible benefits of extrapair paternity in socially monogamous species, such as "good genes" for offspring or genotypic diversification as a hedge against environmental unpredictability. Feminist scientists like Zuk may be entitled to say "we told you so," but developments in science, not ideology, have made it possible for them to say it.

Ultimately, although Zuk draws attention effectively to the dangers of anthropomorphism, her message on the role of ideology in scientific research is rather confused. On the one hand, she asserts repeatedly that "feminism has more to offer biology than vice versa," since it can, for example, help keep science "honest" (by ensuring that it focuses on phenomena that are not merely "sexist spandrels"). On the other hand, she acknowledges that "taking an ideological stance" can actually *prevent* researchers from asking interesting questions. With the benefit of hindsight, we see that male behavior is only half the story, but it does not follow that what science needed all along was a healthy dose of feminism. In the end, it isn't clear in which direction the majority of insight has flowed. Feminism seems to have more to offer to biologists than to biology itself, but biology clearly has a great deal to offer feminism.

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DO ANIMALS HAVE GENDER?

Evolution's Rainbow: Diversity, Gender, and Sexuality in Nature and People. Joan Roughgarden. University of California Press, Berkeley, 2004. 474 pp. $27.50 (ISBN 0520240731 cloth).

Soon after transitioning as a transgendered woman, Joan Roughgarden, professor of biological sciences at Stanford University, undertook a book-writing project to celebrate and explain diversity in sexual presentation. To do so, she explored all aspects of sexual reproduction, including the sexual behavior of animals, the development of human sex differences, and the varied role that gender plays in world cultures. As she became deeply engrossed, how-

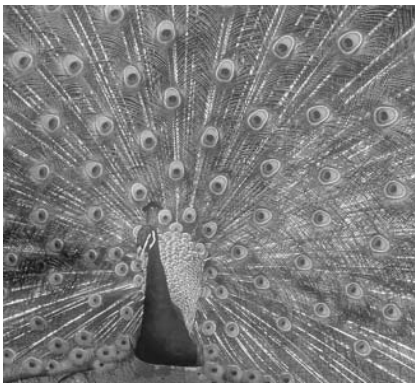
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ever, Roughgarden also concluded that experts in each of the academic disciplines she explored were disparaging of diversity. Particularly in her home fields of evolution and ecology, she found "diversity in gender and sexuality denigrated by sexual selection theory, a perspective that can be traced to Darwin." So in addition to celebrating diversity, she determined to set the record straight and to proclaim that "Darwin's theory of sexual selection was false" (p. 5).

Because my interests are in animal behavior and sexual dimorphism, I was preadapted to enjoy the book, and enjoy it I did. The style, informal and personal, makes it highly readable, and the numerous facts and controversial ideas it presents are certain to stimulate future research. I came away more convinced than ever that, when it comes to sex and gender, we are not all alike. That said, I also found the book frequently annoying and occasionally infuriating, in part because of the author's relentless stereotyping of the academy.

The author convincingly builds her case that animals frequently deviate from simple stereotypes about sex differences. Female animals are not always coy and nurturing, nor are males always big, colorful, and aggressive. In fact, females are commonly the larger sex, and in some vertebrates, they are dominant to nurturing males. In two extreme examples, female spotted hyenas possess a penis-like clitoris that they erect during social interactions, and the female blue-headed wrasse, a fish, can change sex from female to male.

But somehow her review of the inadequacy of popular stereotypes leads Roughgarden to conclude that Darwin was wrong about sexual selection, and on this point she fails utterly to convince me. Darwin sought to account for all sex differences by attributing the origin of some to a process that "depends on the advantage which certain individuals have over other individuals of the same sex and species, in exclusive relation to reproduction" (Darwin [1871] 1981). The peacock's tail is the classic sexually selected trait, but Darwin was aware that in some systems females, not males, compete for mates. In these exceptional systems, the



"sex roles" are reversed, and brightly colored, aggressive females leave the care of offspring to males. Darwin's powerful insight did not make him a champion of women—hardly (see, for example, Darwin [1871] 1981, p. 327). But it's Darwin's ideas on sexual selection that are on trial in Roughgarden's book, not his attitudes toward women, and his ideas have stood the test of time.

I grant that there has been excess in the name of Darwin. Like Roughgarden, I too have experienced impatience or embarrassment with the language of behavioral ecology, including the oversimplification of the evolutionary process, the annoying tendency to speak of genes as being "for" this or that, and, perhaps most of all, the presumption of "good genes." Some researchers who study animal behavior have certainly been carried away with the iconic contrast between the supposedly bold, aggressive, sexually rapacious male and the passive, dependent female. But I know of others who have quantitatively explored the evolutionary implications of sex differences in the opportunity for selection (Shuster and Wade 2003). These scholars and many others do not receive their due.

The book makes five additional important assertions. First, Roughgarden states that evolutionary biologists have overemphasized the role of competition in explaining behavior and have underestimated cooperation. She claims that evolution can give rise to group-level, cooperative adaptations that promote sexual access, without relying solely on reciprocal altruism or kin selection, through a process known as social selection. This troubling aspect of the book is presented as novel and straightforward, when it is neither. Second, Roughgarden argues that sexual differentiation is a complex but comprehensible subject that involves the interaction of many genes that lead to numerous equally viable and stable outcomes, which medical scientists have failed to appreciate as normal. Rather, they have made pathologies of healthy departures from the norm. This section of the book is extremely effective. The book's third assertion is that, like animals, humans form a rainbow of diversity in their sexual presentation, and that while anthropologists and social scientists have successfully cataloged this variety, they have too often treated Western culture as the norm and denigrated diversity. The fourth and fifth assertions are the ones I found most intriguing, namely that animals have gender, and that while animals come in only two sexes, based on the size of their gametes, they often come in more than two genders.

Do animals have gender? Over the past few years I have objected to the substitution of the phrase "gender differences" for "sex differences" in biological writing. When asked, my colleagues in the Department of Gender Studies agreed that the term *gender* could be properly applied only to humans, because it involves one's self-concept as man or woman. Sex is a biological concept; gender is a human social and cultural concept. But Roughgarden defines it this way: "Gender is the appearance, behavior, and life history of a sexed body" (p. 27).

In reading this book, I realized that the distinction between sex and gender (i.e., between gonadal sex and external phenotype) might be useful and informative when applied to animals. Typically, I determine the sex of the animals I study by examining their external morphological or behavioral phenotype. In the dark-eyed junco, a songbird, males are darker, bigger, and have whiter tails than females. They also sing, but they do not produce precopulatory displays, build nests, develop a brood patch, or incubate eggs. Females are their opposite in all these attributes. To be certain in my determination of a bird as a male or a female, I can inspect the gonads or use a molecular technique to verify the pres-

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ence or absence of a marker on a heteromorphic sex chromosome. But a multivariate statistical technique can properly classify 95 percent of juncos as male or female simply on the basis of body size and plumage, and this method will typically suffice, because morphological and behavioral sex are so nearly identical to gonadal and chromosomal sex.

But what of that 5 percent that cannot be classified by size and color: Does their "intermediate status" not demand an explanation? And how reliable were the additional external criteria I relied on? Having observed many thousands of juncos by now, I have seen most of these criteria break down. I have encountered many dark females and small males, as well as a few males that helped to build a nest or incubated eggs. On the other side, I have heard females sing, and seen them court other females when treated with testosterone. This leaves brood patches and egg laying as the only strictly female characteristics in juncos. These may connote sex, but all the rest could fairly be called indicators of gender, suggesting that ambiguous individuals deserve more focused study.

Can there be more genders than sexes? Roughgarden posits that while animals come in only two sexes, many species have more than two genders. How can this be? Sex refers to the size of the gametes, and, quibbling exceptions aside, sexually reproducing species have only two types of gamete, big and small (eggs and sperm). Salmon, sparrows, and damselflies, however, are examples of species with multiple, recognizable external phenotypes that cluster by body size or color, which Rougarden calls "genders." Again, I asked my colleagues who study gender in humans about this idea, and one reaction was, "Why do we need more categories? I thought we were trying to get away from categories." While I agree with that, I also agree that multiple genders are a logical extension of Roughgarden's definition. Recognizable by their definable phenotypes, they are the raw material of further evolution and demonstrate that there is indeed more than one way to be a male or a female. I'm not sure what will follow from this novel form of description, but think it bears watching.

To conclude, this is a provocative book that prompted serious introspection and a renewed desire to sift the good from the bad in my discipline. The author has synthesized huge, interdisciplinary literatures, and interpreted them in relation to her theme that diversity in sexual presentation is everywhere and is incompletely appreciated and understood. For this she is to be admired. Any book that promotes tolerance through knowledge is welcome; unfortunately, one that does it by stereotyping the opposition loses some of its force.

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THE LIFE AND TIMES OF A LIVING FOSSIL

The American Horseshoe Crab. Carl N. Shuster Jr., Robert B. Barlow, and H. Jane Brockmann, eds. Harvard University Press, Cambridge, MA, 2004. 427 pp., illus. $95.00 (ISBN 0674011597 cloth).

Each spring, unnumbered thousands of American horseshoe crabs (*Limulus polyphemus*) approach the edge of

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the sea and emerge from quiet estuaries to lay eggs on intertidal beaches on the continent's Atlantic and gulf coasts, thus perpetuating an extraordinarily ancient life history. The American horseshoe crab, a "living fossil" that ranges from Maine to the Yucatán, is one of four extant representatives of the xiphosurans (horseshoe crabs and their extinct relatives), whose basic body plan has persisted for some 400 million years. The continued success of this marine species is remarkable in light of its risky intertidal sojourn, which makes it highly visible and vulnerable to terrestrial predators. On spawning beaches, shorebirds consume horseshoe crab eggs to fuel their tenuous migration, and watermen following a traditional way of life collect horseshoe crabs for bait. Fittingly, those competing pressures are where *The American Horseshoe Crab* begins and ends. In between, readers of this multiauthored book, edited by Carl N. Shuster Jr. (adjunct professor, Virginia Institute of Marine Science), Robert B. Barlow (director of vision research, State University of New York at Syracuse), and H. Jane Brockmann (professor of zoology, University of Florida), will find chapters on a wide range of topics by prominent researchers who share an abiding interest in this remarkable creature.

The authors' stated goals were to address "highlighted topics" and answer commonly asked questions on this most researched of all marine arthropods. The authors also set out to make the book accessible to a wide audience. The book's topical coverage is extensive, but the degree to which topics are accessible to a nontechnical audience is inconsistent. The language and information in different chapters range from the elementary to the technical. Glossaries are attached to the more technical chapters, and exhibits provide helpful background material. In contrast, the previous major edited volume on horseshoe crabs (Sekiguchi 1988) was organized under major headings, covered all four extant species of horseshoe crabs, and was written for a technical audience. Although *The American Horseshoe Crab* has a somewhat random organization typical of edited volumes, it has many accessible entry points, depending on the reader's interest and background.

The American Horseshoe Crab opens with a chapter by Mark Botton and Brian Harrington on the horseshoe crab–shorebird relationship. The chapter is devoted largely to migrant shorebirds and their brief stay in the Delaware Bay, where high densities of spawning horseshoe crabs cause initially buried eggs to surface and become available to the foraging birds. Increases in horseshoe crab harvest, coupled with declines in the spawning biomass of horseshoe crabs and in the abundance of shorebirds (the red knot [*Calidris canutus*] in particular), have prompted the development of a coastwide management plan, which is the topic of the book's last chapter.

The breadth of the topics covered and the thoroughness of the material presented in The American Horseshoe Crab *ensure that the book's value, like its subject, will persist.*

In chapter 6, Botton, Shuster, and John A. Keinath continue the discussion of food webs and introduce the topic of epibionts. If you spend time watching horseshoe crabs on the beach, you'll notice a diverse assemblage of sessile organisms (epibionts) that use them as substrate. Allee (1922) summed it up by referring to the adult horseshoe crabs as a "walking museum."

The two chapters by Brockmann on reproductive ecology and behavior hit the mark by targeting a broad audience exceptionally well. In chapters 2 and 3, Brockmann outlines for the reader in clear, straightforward prose what is known about horseshoe crab behavior and instructs the reader on the science behind the knowledge. She is careful to address the question, "How do scientists know that?" as she provides a narrative on horseshoe crab nesting behavior. For example, as Brockmann describes how females move through the sand to bury multiple clusters of eggs, she hints about how easy it is to track the progress of a nesting female using surveyor's flags. She makes it sound so easy that any reader can envision him- or herself participating in the scientific discovery.

No book on the horseshoe crab would be complete without a thorough discussion of limulid evolution. Shuster and Lyall I. Anderson coauthor two chapters that interweave evolution and natural history. In chapter 7, they use an analysis of the body plan to discuss how *Limulus* interacts with the physical environment and how it compares with other horseshoe crabs, both living and extinct. The horseshoe crab's persistence has been attributed to its generalist nature. However, Shuster and Anderson infer in chapter 8 that, with few exceptions, the distribution of horseshoe crabs has been tied to estuaries and associated spawning habitats through geologic time.

The book highlights the special contributions that studies of horseshoe crabs have made to human health. In chapter 4, Barlow and Maureen Powers engagingly summarize more than 70 years of vision research that has used *Limulus* as a model. Researchers have explored the horseshoe crab's remarkable ability to increase retinal sensitivity at night, described the role of vision in horseshoe crab mating behavior, and discovered mechanisms by which the brain interprets visual information. Work on horseshoe crab vision by H. Keffer Hartline, who shared the Nobel Prize for vision research with Ragnar Granit and George Wald, has led to understanding of basic mechanisms of vision common to all species.

Undoubtedly the best-known link between human health and horseshoe crabs is *Limulus* amebocyte lysate (LAL). LAL is the substance from horseshoe crab blood cells that causes clotting when exposed to bacterial endotoxin. The LAL-based bacterial endotoxin test (or gel-clot test) is the gold standard for detection of bacterial contamination in injectable drugs and implantable medical devices. In chapter 13, Jack Levin, H. Donald Hochstein, and Thomas J. Novitsky organize their thorough review of LAL development into three parts: discovery, development of standards and regulations, and commercialization. Chapters on the circulatory system (chapter 11 by

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Shuster) and the immune system (chapter 12 by Peter B. Armstrong) provide important background material for the LAL story. From the late 1970s to the early 1990s, research on LAL became a focal point for horseshoe crab researchers worldwide, contributing broadly to horseshoe crab biology. The chapter ends with a note that the LAL gel-clot test might someday be replaced by a genetically engineered version or other biochemical alternative.

Basic horseshoe crab biology is covered in several chapters on development and growth (chapter 5 by Shuster and Koichi Sekiguchi), physiology (chapter 9 by David W. Towle and Raymond P. Henry), and disease (chapter 10 by Louis Leibovitz and Gregory A. Lewbart). Overall, these chapters, along with the chapters on circulatory and immune systems, were more technical in nature and will serve as valuable references. The chapter on disease includes previously unpublished discoveries based on Leibovitz's research and veterinary practice at the Marine Biological Laboratory.

Sprinkled throughout the book are personal recollections on what stimulated researchers' interest in horseshoe crabs. In a couple of cases, accomplished scientists found their research subjects by literally happening across them. Shuster and Sekiguchi, who are recognized as fathers of modern horseshoe crab biology, share brief biographical sketches describing career paths that led them to lifelong studies of horseshoe crabs.

The book closes with a chapter on horseshoe crab conservation by Shuster, Botton, and Robert E. Loveland. Before 1999, conservation and management were inconsistent and highly localized. Concern over the possible effects on shorebirds of dramatic increases in the harvest of horsehoe crabs as bait for whelks (*Busycon carica* and *Busycotypus canaliculatum*), together with the loss of spawning habitat, has prompted fisheries managers to formulate a coastwide management plan (Atlantic States Marine Fisheries Commission 1998). Since the book's publication, harvest in the Delaware Bay region has been reduced to 25 percent of the peak harvest that occurred during the late 1990s . The authors appropriately acknowledge watermen's efforts to conserve horseshoe crabs by adopting bait-saving practices. One important conservation measure carries the name of the senior author. The Carl N. Shuster, Jr. Horseshoe Crab Reserve was established in 2000 to protect horseshoe crabs on the continental shelf off the mouth of the Delaware Bay. Hopefully, the implementation of the coastwide management plan and efforts to reverse the decline of shorebirds will be successful, and a reader 20 years from today will find it odd that a book on horseshoe crabs begins with a chapter on shorebirds.

The breadth of the topics covered and the thoroughness of the material presented in *The American Horseshoe Crab* ensure that the book's value, like its subject, will persist. In my opinion, the authors have achieved what they set out to do. A wide audience will turn to *The American Horseshoe Crab* to answer common and not-so-common questions about a truly remarkable creature.

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