Ultraselfish Symbionts

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Sex Wars: Genes, Bacteria, and Biased Sex Ratios. Michael E. N. Majerus. Princeton University Press, Princeton, NJ, 2003. 280 pp., illus. $45.00 (ISBN 0691009813 cloth).

To paraphrase Robert Ricklefs, it is remarkable how many populations have a 1:1 sex ratio—and how many exceptions there are to this rule. To me, even more remarkable is that we now understand the evolutionary forces that produce the rule, as well as the forces that produce most of the exceptions. This triumph of 20th-century science has provided perhaps the best case for a selfish-gene view of life. In *Sex Wars,* Michael Majerus, a Cambridge entomologist, argues that some of the exceptions are explained not just by an organism's own genes but also by the genes of its inherited microorganisms.

In many species, mothers pass a veritable zoo of microorganisms on to their offspring, including bacteria, microsporidia, and mycoplasmas. These live in cell cytoplasm, and because almost all cytoplasm in offspring is derived from the mother, a microorganism that ends up in the cytoplasm of a male is going nowhere. The heart of this book is concerned with how these organisms usurp their hosts to avoid that dead-end outcome.

It is great stuff—it can hardly fail to be, given the fantastic natural history involved, so much of which has been learned in the last decade or so. In retrospect, much of it could have been predicted. As a maternally inherited microorganism, what options do you have for avoiding the black hole of life in a male? If you are unlucky enough to get into a male, you could turn him into a female. If you cannot do that, you could kill him, if that releases resources for his sisters that are infected with your sisters. Or you could kill him and try to transmit yourself from his corpse to another host. Better yet, perhaps you could force your host to abandon producing male offspring altogether and become parthenogenetic. Then you would get into all of her offspring.

All these options have been exploited by some microorganisms. *Wolbachia* species, a group of gram-negative bacteria, have the widest repertoire. They are adept feminizers. In the case of one wood louse species, they have proved so good at their work that some populations are all genetically male, with the feminizing *Wolbachia* keeping the host species going. Other species of *Wolbachia* also induce parthenogenesis and kill males. In one African butterfly species, male-killing by *Wolbachia* has meant that just 5 percent of the population is male. Curiously, the advantage of male-killing remains unclear in that case.

The advantage of male-killing in ladybirds is well understood, thanks to work that Majerus himself has conducted. An array of microorganisms are involved, including *Rickettsia, Spiroplasma,* and *Wolbachia,* as well as unknown flavobacteria and γ-protobacteria. All these can be male-killers. The explanation for this suicide is simple. Ladybird larvae eat eggs that fail to hatch. This gives them a nutritional advantage early in life. Male-killers prevent male eggs from hatching, thus increasing the fitness of their clone mates in the sisters of their dead host.

All of this must have some fairly profound evolutionary consequences for the host. Majerus speculates on many of these, but makes it very clear that there is little supporting evidence. For instance, in a species with 95 percent females, there must be huge selection pressure on uninfected hosts to produce highly male-biased sex ratios. Similarly, parthenogenesis could be a way of keeping a host lineage free of these symbionts.

One of the book's strengths is that speculations are liberally sprinkled about. For instance, where sex is determined by the sperm chromosomes, symbionts should not want the egg they are in to be fertilized by male-chromosome-bearing sperm. Do symbiont-infected eggs thus reject male sperm? There is no evidence either way, but as Majerus points out, the ingenuity with which these organisms achieve their goals cannot be overestimated.

Ultraselfish elements are intrinsically interesting, with a fascinating natural history and great theory. Yet the excitement struggles to emerge from *Sex Wars.* A third of the book describes sex, sexual selection, sex-determining mechanisms, and the like, in a level of detail that is not needed to understand the symbionts. Indeed, the only aspect of this that I found interesting was a refutation of the divine explanation of 1:1 sex ratios—and what made that interesting was that there apparently is a divine explanation (Adam, Eve, the ark, etc.), and that Majerus's refutation of it was so uncompelling.

Indeed, it is not really clear for whom the book was written. It is not a research monograph or a racy popular science book (despite the title, it is far too dry and jargon laden to be racy), and I cannot quite envisage the undergraduate course that could be built around it. Half the book would be great for a graduate course, but any PhD student in evolutionary genetics should already know the remaining content.

Nevertheless, I hope graduate students do read this book. It makes painfully clear how few people are working in this field and how important new molecular technology is going to be in sorting things out. Majerus clearly feels that inherited symbionts are going to figure large in accounts of host evolution. The jury is still out: They may turn out to be just weird

oddities. But given how much so few have found out with so little, he may prove to be correct. What is very clear, though, is that modern evolutionary analysis has the power not only to explain the natural history revealed to Victorian vicars but also to understand the radical natural history being uncovered today.

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A LONGING LOOK AT THE GREAT PLAINS

Great Wildlife of the Great Plains. Paul A. Johnsgard. University Press of Kansas, Lawrence, 2003. 309 pp., illus. $29.95 (ISBN 0700612246 cloth).

The Great Plains are changing as the nation changes. City folks are buying up the scenic parts at fantastic prices and questing for the mythic cowboy lifestyle. Farmers and ranchers are eking out a living at best, using pivot irrigation or, in many places, abandoning what used to be great plains. Meanwhile, an increasingly urban US population looks on with ever-diminishing knowledge of nature, and with little idea of what the Great Plains used to be. This home where the buffalo roamed is the subject of Paul Johnsgard's *Great Wildlife of the Great Plains.*

Written in the style of a naturalist's notebook, *Great Wildlife* is a work of sensitivity, beauty, and elegance. With chapters centered on particular habitats ("Shaded Shorelines and Tall Trees") or taxa ("Waders, Dabblers, and Divers"), Johnsgard gives us a view of the plains that is wistful and longing, seeming more like an early 20th- than an early 21st-century account. This book covers hundreds of taxa, giving facts, figures, and personal observations. We're given a tour through many years of Johnsgard's field notes, backed by the authority of his long career of scholarly research.

Although some species are briefly mentioned in long lists (which could prove tiresome to a reader not familiar with the taxa), other species are carefully described with the professional naturalist's keen eye, developed from long personal observation. The author takes us with him to a blind to observe lesser prairie chickens, to the Black Hills to look at Townsend's solitaires, and to the Nebraska Sandhills to find tiger salamanders. Moving rapidly from one species to another, the author is at times quite deft and at times less so. The smooth transition from goshawk to ruffed grouse works smoothly—"One of the favorite prey of goshawks is the ruffed grouse." But after a section on peregrine falcons, the author moves to barn owls with the awkward segue, "Like peregrines, barn owls have different nest-site tendencies now than they did in presettlement times."

I found very few errors, chiefly typographic or editing lapses. On page 10, for example, the author refers to the upland plover, but two pages later he uses the more recent name "upland sandpiper." A mention of North Pass on page 116 apparently refers to Wyoming's famous South Pass. A few factual errors slipped in: For example, the reintroduction of black-footed ferrets to the Shirley Basin of Wyoming has had problems caused by plague, but it has not failed, as Johnsgard states.

The language is spare and elegant. "Although usually silent, during spring the marshes of the Dakotas and Nebraska fairly ring with the tinkling calls of western grebes, resembling sleigh bells in the distance." Perhaps so—but most people today are hearing neither sleigh bells nor grebes. And that was the one problem I had with this book. I read *Great Wildlife* with a growing and maddening sense of claustrophobia, knowing that these things are rapidly disappearing. I began to feel

that I was seeing final glimpses of a world gone by. Although not gloomy on the surface, the book is a litany of what we have lost and continue to lose.

Each species highlight is followed by the sad facts. Under grassland sparrows we learn that "the estimated rate of national decline in the Henslow's sparrow was the third greatest of all 424 species analyzed." And "with its many diverse ecological connections, it was inevitable that the sad history of the prairie dog would be reflected in the fortunes of many other high plains species. The mountain plover, swift fox, and black-footed ferret are now all variously threatened or endangered at state or national levels." In an unemotional, factual way, Johnsgard spells it out for species after species: down by this amount or reduced to this small area. The tallies of percentages lost, breeding declines, and acres converted are chilling.

Johnsgard is an evocative storyteller. Each natural history gem leaves you longing for the experience: "Small spruce trees seem to be a favorite winter roost site [for saw-whet owls], and it is always a special thrill to peer into a snow-covered spruce and see a tiny owl intently staring back at you." In my 48 years as a birder, I have seen perhaps three saw-whet owls staring out of trees in the manner Johnsgard describes. I've whistled in more than that number by imitating their calls. And I've caught enough of them in mist nets to know that they're still out there in larger numbers than nonbirders would suspect. But how many people in our society have ever seen one? How many people know that a thing called a saw-whet owl even exists? We're at the point where only serious naturalists can see nature as Johnsgard does, and then only with luck. For most Americans, these species no longer exist. Although 19th-century natural histories were full of such anecdotes, the 21st-century reader has a sinking feeling that these accounts will soon sound—may already sound—like a Catlin account of American Indians on the plains.

The book's last chapter, "What is Still So Great about the Great Plains?" is the saddest of all. It doesn't conclude that the Great Plains are doomed, nor does it argue for solutions such as the "Buffalo Commons" (Callenbach 1996). Instead, Johnsgard again tallies the enormous habitat losses and directs the reader to an appendix listing the few places you can still go to see the remaining shards of what was once our nation's grandest treasure.

And grand it was. When Lewis and Clark crossed the Great Plains in 1805, they saw a landscape unimaginable today: "emence numbers of antelopes in the forks of the river, Buffalow & Elk & Deer is also plenty. Beaver is in every bend." The bison are now obviously gone, but it is less obvious how much the rest of the ecosystem has declined. Because of farming and ranching practices, today's Great Plains are a pale ghost of what they once were. It is not only that the large predators have all been exterminated from the Great Plains; there are also fewer animals present, because the food web has been truncated, "unpopular" animals persecuted, weeds spread, the landscape fragmented, and water diverted to cattle and their feed (Freilich et al. 2003).

This book should spur readers to action. Reading *Great Wildlife* was a visceral reminder that past conservation practices have failed us. Now is the time to change our strategies. Perhaps bison and wolves will again one day move across the Great Plains and bring with them burrowing owls, American burying beetles, least terns, black-footed ferrets, and other species now in danger of extinction. Johnsgard's book gives us a feel of the once and future plains. The Buffalo Commons deserves a try. The Commons is a yet-untried vision in which bison are restored, fences are torn down, and the plains are allowed to go wild. Based in part on potential ecotourism dollars, and at first reviled by ranchers, the idea has persisted and has continued to gain credence. At least one or two national grasslands should be set to the task and nearby ranchers invited to join in. The vision could be realized if enough people willed it to be. In the meantime, *Great Wildlife of the Great Plains* is a lovely and engrossing read about what might have been.

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(Editor's note: Jerry Freilich is an employee of the National Park Service, but the views expressed in this review are his own and do not nececessarily reflect the views of the US government.)

FROM FIBER TO FEEDSTOCK TO FOSSIL FUEL REPLACEMENT

Biorenewable Resources: Engineering New Products from Agriculture. Robert C. Brown. Iowa State Press, Ames, 2003. 286 pp., illus. $74.99 (ISBN 0813822637 paper).

Recent years have seen a remarkable growth of interest in the use of biologically produced fuels and materials, in part because of concerns that humans have become overreliant on fossil fuels and in part because of apprehension about increasing atmospheric levels of greenhouse gases. Although several academic disciplines address aspects of the emerging field of biobased resource utilization, industry needs employees with an appreciation of how these disciplines can be integrated. Until now, textbooks have seldom offered the broad perspective necessary to train students to conduct research and be effective managers in this growing field. Robert C. Brown's fine book fills this gap by providing a logical overview of the relevant areas of engineering, thermodynamics, and

chemistry, as well as a clear account of the range of raw materials and processes available.

Brown, who holds the Bergles chair in thermal sciences at Iowa State University, is professor of mechanical and chemical engineering and director of the university's Center for Sustainable Environmental Technologies. His book is intended for upper-level undergraduate and first-year graduate students in science and engineering, but I suspect it may well find broader use as a general reference among professionals.

Brown begins by defining what constitutes biorenewable resources—anything containing organic material that uses sunlight for energy, from crops to trees. He then discusses what drives the growing interest in bioenergy and biobased products. Aside from the fears about the greenhouse effect and overreliance on fossil fuels, which lead to national security concerns, are worries about pollution from acid rain and stratospheric ozone depletion. To his credit, Brown does not shrink from describing the challenges that stand in the way of converting a primarily petroleum-based economy back to one at least partially based on renewable resources.

The book provides all the scientific foundation needed for an understanding of how biobased raw materials are converted into finished products. The broad sweep of the work is evident in its treatment of the conversion of a wide range of raw materials to energy and in its description of a wide range of production processes. Brown also considers harvesting and storage of herbaceous and woody crops, ranging from annual cereals, switchgrass, and alfalfa to hybrid poplar and eucalyptus.

Chapters five through eight cover conversion of biorenewable resources into a variety of products, such as fuels, chemicals, solvents, plastics and fibers. Brown reviews furnace designs and explains how they can best be applied in boiler systems, detailing power cycles of relevance to bioenergy. Happily, he provides enough theory for the student to understand how limits to efficiency come about. Brown rightly gives a considerable amount of space to fuel cells, which are one of the recently publicized new energy technologies. Although carbonaceous fuels must first be reformed to hydrogen before they are suitable for use in such cells, the high thermodynamic efficiency of fuel cells makes them attractive when other fuels are relatively costly. Still, the initial requirement for fossil fuel generation of energy does not necessarily help reduce reliance on petroleum or coal.

Almost as many important intermediate chemicals can be manufactured using biomaterials as can be produced with petroleum. Brown presents a list of the top 60 (by annual production) commodity chemicals in the United States and considers which of them can most efficiently be produced with biorenewable materials. This very worthwhile exercise demonstrates that increasing the use of biorenewable materials will depend

more on bringing about changes in the manufacturing infrastructure than on finding new chemical pathways.

Brown evaluates the co-firing of biomass with coal, as well as the other mechanical and chemical processes for producing fuel gas from biomass with heat. He gives a valuable assessment of the potential of anaerobic digestion for producing "biogas," a mixture of methane and carbon dioxide, and provides a full discussion of the production of ethanol, methanol, and "biodiesel" as transportation fuels. His presentation of the arguments for and against the last of these, in particular, is evenhanded. Production of biodiesel entails the chemical conversion of several oilseed triglycerides into methyl or ethyl esters of the fatty acids. The resulting fuel has properties very similar to those of petroleum-based diesel.

Brown concludes that, although the production of the fuel ethanol from starch is straightforward, the economics are critically dependent on efficient utilization of by-products or their conversion to higher-value final products. This insight could well provide opportunities for innovators. For example, conversion of cellulosic, hemicellulosic, and lignocellulosic materials to sugars for fermentation is a critical limiting step for the utilization of many biomaterials; Brown describes several pretreatment processes that can be used to convert cellulose and lignocellulose to fermentable five-carbon and six-carbon sugars, but opportunities to further improve efficiencies at this key process bottleneck still exist.

Chemical building blocks used by the petroleum industry include syngas (a mixture of carbon monoxide and hydrogen), ethylene, propylene, butadiene, and a mixture of monocyclic aromatic hydrocarbons known as BTX (benzene, toluene, and xylene). It is impractical to simply replace these with building blocks derived from biorenewable resources—many are hard to manufacture economically from biological resources—but it may well be feasible to create substitutes. Oxygenated organic compounds can be used as building blocks in the production of fuels and commodity chemicals, for example. The book gives an expert survey of biological and enzymatic processes that can yield such valuable intermediates.

One particularly valuable aspect of this work is that Brown does not give short shrift to the mechanical and chemical pulping processes that are an essential facet of the production of natural fibers. Herbaceous materials contain less lignin than does woody material, which makes pulping herbaceous material easier, but the paper that is produced lacks the strength of paper made from woody raw materials. Needless to say, the considerations quickly become more complicated in more complex processes.

In the latter part of the book, Brown provides a valuable account of the environmental and economic issues confronted by the bioprocessing industry. One of the most exciting new frontiers is the use of genetic engineering to produce materials optimized for efficient use. Despite some public resistance to genetic engineering of crop plants, especially in Europe, Brown is skeptical about one commonly heard argument against the technology: that it will lead to a loss of biodiversity. Agriculture in general leads to a loss of biodiversity, he notes. Moreover, Brown is just as dubious about another feared threat, that transgenes in food crops might jump into human DNA. Although he states that this scenario is highly unlikely, he (surprisingly) offers a diagram that depicts it.

The final two chapters include an effective comparison of biorenewable and fossil-based resources in terms of their nitrogen, sulfur, and chlorine content. Brown demonstrates the use of "life-cycle analysis" to show how it is possible to anticipate the environmental impact of a new product. These final chapters also include an introduction to methods for determining the cost of producing a crop and for analyzing cash flow. In examples, Brown estimates the cost of manufacturing various biologically based chemicals and of producing electricity from several biorenewable resources.

Throughout the book, plentiful illustrations help the student visualize complex processes. Process diagrams are particularly helpful, and problems at the end of each chapter will aid study.

Brown's book is a valuable resource. I found a few typographical errors that could be confusing to a student, but that was the only shortcoming I identified. Teachers, students, and practitioners are fortunate to have access to this impressive compilation on such a vital field.

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NEW TITLES

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