

The Genial Gene: Deconstructing Darwinian Selfishness

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Source: BioScience, 60(1) : 76-78

Published By: American Institute of Biological Sciences

URL: <https://doi.org/10.1525/bio.2010.60.1.13>

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are coupled together by ribosomes, for example, or the process of chromosome reduction in meiosis, greatly complicates the reader's task. To understand mitotic division and comprehend how objects like spindles, poles, and asters perform their functions requires the reader to visualize their architecture and positional relationships. I suspect that the process of gastrulation, whereby the three germ layers are formed and take up their required locations (as outlined in chapter 7), will be virtually impossible for the lay person to visualize from just the verbal account. In a future edition, illustrations, even simple sketches, would enhance understanding.

In the final third of the book, Wolpert moves progressively further from his field of expertise. He tackles neurobiology, including learning, neural nets, and even genetic control of behavior. He discusses differential growth and aging, the latter explained not by genetic regulation but by wear and tear: "an accumulation of unrepaired cellular and molecular damage and the limitations in cell maintenance and repair functions" (p. 147). Subsequent chapters deal with cancer and cellular defenses against disease; "cancer cells break all the rules of cooperation in this happy [cellular] community" (p. 177). Other diseases like cystic fibrosis, sickle cell disease, or muscular dystrophy result from gene mutations or other "mistakes in the society of cells." The last chapter attempts to deal with evolution and the origin of life but ends realistically and with a tangible sense of disappointment: "Even though our cells' origins remain uncertain..."

In a sense, these final chapters are the most interesting, in that they stray beyond the orthodoxies of experimental science. The author is fearless in offering opinions. For the Catholic church's decision that the soul enters the fetus at conception, Wolpert questions with Anne McLaren how many of those who believe the fertilized egg to be a human would ignore the cries of a baby in a burning building and choose instead to save a hundred frozen eggs. In discussing the ethics of human cloning: "I have offered a prize bottle of champagne to anyone who could show me

that cloning a human being raises any new ethical issues" (p. 116). Regarding creationist views of the beginnings of life: "There is no evidence whatsoever for such a creator or designer, but those who believe that there is one have no need to think hard about the origin of life" (p. 215).

When I was in my early teens a favorite uncle gave me a copy of Hendrik Willem Van Loon's *The Story of Mankind*. This now-famous book begins with an image of an enormous rock, a hundred miles high and a hundred miles wide. Once every thousand years a little bird comes to this rock to sharpen its beak. When the rock has thus been worn away, then a single day of eternity will have gone by. That image—whimsical, powerful, accessible—was one of my early "aha" moments, giving me a new way to think about time and about the world. Lewis Wolpert's *How We Live and Why We Die* is described in the publishers blurb as "an accessible guide to understanding the human body and, essentially, life itself." I read the book, hoping to find a story filled with powerful images that I might give to my teenage granddaughters, to lead them to some new ways to think about living things. Professor Wolpert's "society of cells" is only partially successful in achieving that admittedly demanding goal.

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DID YOU COMPETE OR COOPERATE TO FIND YOUR MATE?

The Genial Gene: Deconstructing Darwinian Selfishness. Joan Roughgarden. University of California Press, 2009. 272 pp., illus. \$24.95 (ISBN 9780520258266 cloth).

Unless you're Brad Pitt or Megan Fox, attracting mates can be a complicated process, and most will agree that some degree of competition is involved. Limited resources of value, whether they be other people, places to live, or food, will lead to competition among individuals or societies that attempt to secure them. Whether it is good or bad, natural or unnatural, competition underlies much of the current human condition.

To see what this has to do with Joan Roughgarden's book, *The Genial Gene: Deconstructing Darwinian Selfishness*, some history is useful. Charles Darwin proposed the theory of sexual selection as a corollary to natural selection because he recognized that animals possess many traits that appear detrimental to survival, such as encumbering decoration and gaudy coloration. He proposed that such traits are beneficial, even if they reduce survival, if they confer a long-term advantage in terms of relative mating success. Darwin recognized that such an advantage could accrue either because elaborate traits determined the outcome of male-male competition or because females preferred them.

The theory of sexual selection was largely discounted for 75 years or so, because although biologists (most of whom were males) agreed that male-male competition was obvious, they mostly disagreed that females actively influenced the distribution of mating. Yet over the last 50 years, biologists have documented time and again that female choice is often the most important process determining who mates with whom. Since this realization, evolutionary biologists and behavioral ecol-

doi:10.1525/bio.2010.60.1.13

ogists have embraced sexual selection as critical to understanding both morphological and behavioral diversity. The underlying premise that organisms compete for a limited resource, which determines success or failure in reproduction, is central not only to sexual selection but to many other ideas about the evolution of life.

In *The Genial Gene*, Roughgarden argues that we have it all wrong. Even Darwin had it all wrong, she holds: Sexual selection is “out” (as an intact theory). Also wrong is everyone who thinks that competition was important in the evolution of anything to do with sexual reproduction, the evolution of male and female gametes, secondary sexual traits, morphological differences between males and females, mating systems, parental care, enlarged brains in humans, and human attractiveness (to list just some areas). This is no small challenge. The author argues that almost 100 years of research on sex has, at some level, been misguided. Where have we all gone wrong? Roughgarden believes our mistake was being seduced by competition as a force underlying social behavior and sexual reproduction. What is the alternative? The author is convinced it is cooperation, and she expands on a theory of social selection (originally proposed by Mary Jane West-Eberhard) that she hopes will replace sexual selection.

Take mating systems, for example. The standard view is that whether a species is socially monogamous or polygamous is the result of a basic conflict of interest between the sexes (males attempting to mate with many females, females attempting to secure resources), and how this conflict is resolved in different ecological situations. Roughgarden instead argues that a species mating system is the result of cooperation between the sexes for the mutual benefit of both males and females in terms of successfully rearing offspring. The author acknowledges that competition exists, although she discounts widely accepted examples of conflict as cases of anthropomorphic exaggerations. Instead, she believes that the notion of a conflict of interest between the sexes is a “fad” rather than an underlying para-

digm. Similarly, proponents of sexual selection generally acknowledge examples of cooperation in reproduction. The question that Roughgarden repeatedly raises, however, is: What is the prevalent state? Did sexual interactions evolve as a result of competition, with cooperation occurring rarely; or, as the author argues, is cooperation the common condition, with competition arising only under special circumstances? The question is anything but hair-splitting.

Any member of the educated public will grasp the basic ideas in the book, but The Genial Gene is clearly directed at those biologists who subscribe to sexual selection as a guiding principle. Roughgarden is on a mission to convince them that they have been misled.

The Genial Gene is a relatively short book (255 pages) in which to take on the entire discipline of sexual selection and social behavior, but it is just one in a collection of publications in which the author presents her case for cooperation and diversity. The natural history observations that underlie much of Roughgarden’s social selection theory are summarized in *Evolution’s Rainbow* (University of California Press, 2004 and 2009), and specific applications of the theory are detailed in many scientific publications. The author makes it clear in this book that more is yet to come.

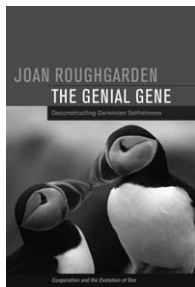
Any member of the educated public will grasp the basic ideas in the book, but *The Genial Gene* is clearly directed at those biologists who subscribe to sexual selection as a guiding principle. Roughgarden is on a mission to convince them that they have been misled. She appears to face an uphill climb. For example, a 2006 paper by the author and colleagues in the journal *Science* (in which they present cooperation models as alternatives to sexual selection) brought several dozen criticisms from leading authorities in sexual selection.

This book consists of three parts. In Part I, “Cooperation and Teamwork,” the author presents her case that the theory of sexual selection is dead and outlines social selection. I found this part to be the most difficult to accept. Yes, the theory of sexual selection has problems explaining some behaviors; however, just as the theory of natural selection has been frequently modified (for example, to accommodate kin selection), so has the theory of sexual selection been modified as new data and ideas have come to light. The author’s implication that sexual selection always refers to “passionate males” and “coy females” is wrong, given that it is well known that sometimes males invest more into raising offspring than females.

Additionally, in my opinion, the author carefully picks out research results that are difficult to explain by sexual selection, and ignores results that support it. Mate choice is an example, or specifically, the female choice for traits in males. In cases where males provide physical resources, theory suggests that females should evolve a preference based on these resources, and this preference has been observed in many studies. Roughgarden ignores these. Sexual selection theory has more difficulty accounting for cases where males provide only sperm; the evolution of female choice in these circumstances has been debated for 40 years. But, even if this “paradox of the lek” has not been completely resolved, the underlying premise of sexual selection (that the choosy sex should be careful in mating decisions) is not necessarily wrong.

Part II is “The Genetic System of Sex.” Here the author outlines alternative theories for the evolution of sexual reproduction: why sex evolved, why there are only two gametes, and why there is diversity of sexuality (male vs. female, hermaphroditism, etc.). I found this section quite enlightening. The author points out some plausible alternatives to standard explanations. For example, the standard explanation as to why sexually reproducing species have one large gamete (egg) and many small gametes of the other sex (sperm) is that disruptive selection on gamete size

occurred through conflict among individuals producing gametes. But Roughgarden summarizes other models for the evolution of sperm and egg that do not rely on conflict.



Part III is “The Social System for Sex,” in which the author examines behavioral systems and asks whether theoretical questions are better tackled by a competition-based approach (e.g., considering evolutionarily stable strategies) or by a cooperation-based approach (e.g., Nash bargaining solutions). There are many game theoretic approaches to behavioral questions, and biologists should indeed consider all possible models. This part concludes with a chapter summarizing how Roughgarden’s view affects a wide range of evolutionary questions.

The book ends with a section on evolutionary psychology and human sexual behavior that I consider a mistake. Roughgarden takes on subjects as wide ranging as secondary sexual characters, gender multiplicity, homosexuality, human attractiveness, the human brain, and rape without adequately introducing them and incorporating them into her main theme. It seems almost as though the author didn’t have the time or space to deal with these issues but felt they needed to be mentioned. I left this section thinking that the author was as guilty of assuming that cooperation explains everything as are proponents of sexual selection when they assume that competition explains everything.

What is the bottom line? Even though I disagree with the author on some points, and though in some cases Roughgarden does her ideas a disservice by discounting well-documented observations of sexual conflict, I applaud her

for shaking things up. I believe she is correct in some of her criticisms, and we should remember that competition in sexual interactions is an assumption that should be tested, rather than a factual starting point. We all need to be more careful in our thinking.

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AN ANT CORNUCOPIA, TRANSLATED

The Lives of Ants. Laurent Keller and Élisabeth Gordon. Oxford University Press, 2009. 256 pp., illus. \$27.95 (ISBN 9780199541867 cloth).

The Lives of Ants is an eclectic, personal book aimed at introducing ant biology to the masses. It is the collaboration of Laurent Keller, a leading sociobiologist and myrmecologist at the University of Lausanne, and the science journalist Élisabeth Gordon. As Keller and Gordon acknowledge early in the book: “Ants are a trendy thing nowadays.” Unlike other books on the market with more sweeping ambitions, it is clear that they aim for a breezy discourse on all things ants (with entries on film, ecosystems, the tree of life, and electrical engineering along the way). To that end, this collection of 31 short essays is better read in a hammock on an autumn afternoon than in a library carrel. It wanders broadly and lightly. It does not dwell in controversy; instead, it is content to describe Keller’s take on a wide variety of subjects having to do with ants, with a particular focus on his favorite question: Just what holds these superorganisms together and makes them tick?

The Lives of Ants is at its best when it describes scientists—often Keller and his colleagues—devising experiments and testing hypotheses. One such essay

describes the many studies detailing precisely how *Cataglyphis* ants find their way home in featureless desert. Along the way one encounters researchers digging up nests to tag young ants with paint, later following them as they learn their territory. Other researchers construct mazes with symbols as signposts to test ants’ visual memory (which, it turns out, is amazingly good). Still others test for solar compasses by pasting ultraviolet-blocking contact lenses on ant heads. Such accounts convey how enjoyable and tractable (close equivalents in field biology) insects can be. In chapters like these, one is reminded of Niko Tinbergen or Jean Fabré.

Likewise, Keller enjoys discussing his various collaborations. When he does, there is a detectable uptick in the spryness of his prose (e.g., at one point referring to Gregor Mendel as “the pea plant man”). My favorite chapter is an account of his work with Ken Ross, detailing the genetics explaining why some invasive fire ants have large, diffuse colonies with many queens, while others fit the more usual notion of a colony ruled by a single queen to whom her workers are fiercely, and territorially, protective. I won’t give away the ending, but it involves a single gene, one allele that is classically “selfish,” a smelly protein coded by the gene, and regicide.

The Lives of Ants is less successful (and this happens frequently) when it reverts to simple descriptions of what is currently known, absent the real work of myrmecologists or the milieu in which they struggle (there is often a tell in such chapters: frequent and lengthy quotations). Given the intellectual breadth of myrmecology—as a subject for evolutionary biologists, community ecologists, artificial intelligence engineers, as well as sociobiologists—maintaining a grasp of each field’s puzzles and protocols is a tall order. That said, chapters on the origins of ants, the ecology of invasive species, and the organization of supercolonies like the army ants and leafcutters (pretty juicy stuff and the subject of much ongoing research) don’t have much oomph.

The book’s other failing is in the readability of its prose. For every essay that

doi:10.1525/bio.2010.60.1.14