BEHAVIORAL EVOLUTION

# Mutual Benefits at All Levels of Life

Robert Trivers

**Genetic and Cultural Evolution of Cooperation**
*Peter Hammerstein, Ed.*
MIT Press, Cambridge, MA, 2003. 499 pp. $45, £29.95. ISBN 0-262-08326-4.

*Genetic and Cultural Evolution of Cooperation* is an excellent book on an important subject. It grew out of a June 2003 Dahlem Workshop intended, in the words of editor Peter Hammerstein, "to elucidate the mechanisms and processes beyond kin selection that promote the emergence of cooperation in systems that range from molecules to societies." In this aim, the volume succeeds admirably. The contributors consider cooperation across a wide range of scales, from intragenomic to interspecific. Each topical block of papers ends with a group report (which incorporates discussions involving additional scientists), all carefully edited and organized. Naturally some topics (such as the rich literature on nonhuman primates) are left out, but if you want a very broad view of the subject, treated in some depth, this is your baby.

The chapters on intragenomic cooperation largely concentrate on basic features of genetic systems that may have evolved to limit internal conflict resulting from driving selfish elements (stretches of DNA capable of overreplication at a cost to the rest of the genome). This block includes a first-rate account by Blackstone and Kirkwood of how mitochondrial control of apoptosis (programmed cell death) may affect conflict between mtDNA and nuclear genes. The general area is certain to grow in importance, as is its linkage to the world of cooperation between individuals.

As for cooperation between individuals of different species, you can hardly do better than the superb work on cleaner fish–host relations, summarized here by Bshary and Noë. They combine very detailed field observations on a variety of species and situations with carefully targeted experimental work to reveal a complex system of reciprocal relations. The cleaners' tendencies to cheat—to eat host tissue instead of less-preferred ectoparasites—are controlled by such factors as partner choice, reputation, and so on. On the more theoretical side, you may enjoy a provocative paper by Bergstrom and Lachmann arguing that in interspecific cooperation, factors associated with slow co-evolution will be favored (in contrast to antagonistic relations, in which rapid evolution is expected).

In his chapter in the volume, Hammerstein asks, "Why is reciprocity so rare in social animals?" To me, the question is a trifle premature. Reciprocal altruism in all its aspects is very difficult to demonstrate, especially in nature. For example, it is not sufficient to demonstrate a positive correlation in beneficent acts across pairs of unrelated individuals (which is sometimes achieved). We must also show "contingency": that withholding a benefit by one results in a similar action by the other (which is rarely established). But partial evidence does not mean zero evidence. The beauty of Axelrod and Hamilton's simple rule ("start positive and then do unto others as they have just done unto you") is that even bacteria can play tit-for-tat, and recent work suggests they do exactly that. In addition, there is widespread evidence that contiguous neighbors act more kindly toward each other than do noncontiguous ones (independent of kinship); this suggests some kind of positive feedback based on frequent association. Reciprocal altruism has been studied in nonhuman primates, from the lab and the wild. Reciprocal relations between mated pairs, a potentially very large subject in birds, have barely been explored.

On the other hand, I am impressed by how often the rule "but what have you done for me lately?" seems to apply within other species as it does in our own. It is also noteworthy that the motivation toward reciprocal spite can be so much stronger than that for reciprocal altruism. If you freely gave me $10,000 thirty years ago, I will gladly buy you dinner now and smile in your presence, but there is not a bone in my body urging any kind of equivalent repayment. If, however, you inflicted a minor cost back then, watch out: I may remember that with malicious intensity the rest of my life. The act of forgiveness, of course, is meant to shortcut this spiteful psychology, and recent evidence on positive mental states suggests that doing so will bring immediate health benefits (for example, in improved immune function). But the precise logic by which these traits are being selected remains to be described.

The book also showcases the work of experimental economists, and here we see an interesting phenomenon. Those who have produced some of the most important recent findings on the human sense of fairness seem unable to think clearly about their own work. In a series of fascinating economic games (e.g., Ultimatum) played with real money, they have shown that humans care strongly enough about fairness to punish others at a cost to themselves when these others deviate from fair principles. Because evolution does not favor responses to situations that have not yet occurred, an important question is what these unusual games are presumed to be measuring. If humans show strong dispositions toward fairness in one-shot, anonymous encounters (sometimes against a computer), this hardly means that these dispositions evolved to function in one-shot, anonymous encounters (sometimes against a computer)—any more than we would argue that children's strong emotional reactions to cartoons show that such reactions evolved in the context of cartoons.

**Model market.** On coral reefs from the Red Sea to Australia's Great Barrier Reef, a wide variety of fish visit the small territories of the cleaner wrasse, *Labrooides dimidiatus*.

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To capture the flavor of the error, imagine that Ernst Fehr approaches me in private with a one-time offer: he will split credit for the idea of reciprocal altruism, 80% Fehr, 20% myself. How should I respond? Accept with gratitude or decline with an insult? But if the latter, how will he respond? Calmly walk away or attack me physically? And then what? Social interactions are intrinsically repeat interactions—at least over short periods of time and usually over much longer periods as well. So the natural assumption is that in life we will respond to social situations as if

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there were later repercussions to our actions. Economists have set up situations in which later repercussions have (in theory) been ruled out, and they have warned us of this fact. When we persist in acting as if future repercussions are important, they then argue that their results prove our behavior never evolved with regard to future repercussions.

Not very impressive mentation, but matters only get worse when these, and other, errors are pointed out. Though their own work is lovingly referenced and cross-indexed, they do not cite those with whom they disagree. We read "some have suggested…" (Bowles and Gintis) and "this skepticism, where it is found, is typically based on…" (Fehr and Henrich) without a reference in sight. A habit of selective noncitation can also turn around and bite. Fehr and Henrich claim they have demonstrated "that the widely held view of ancestral human societies as isolated groups, which did not mix or interact with surrounding social groups or strangers, has little, if any, empirical support." But if there is one thing biologists know for certain it is that outbreeding requires migration among groups, whereas these authors have created a system of isolated groups that leads to ever-increased inbreeding. In anthropology, an entire subdiscipline is devoted to the subject of exogamy and its effects on intergroup relations (and has been for more than half a century). And so on. In short, no one believes in the preposterous social system these authors claim is widely accepted. But in failing to think clearly about their own work, they do provide a nice opportunity for others—namely, to integrate their findings into the growing science the rest of *Genetic and Cultural Evolution of Cooperation* describes.

EVOLUTIONARY BIOLOGY

# The Wide Spectrum of Sex and Gender

**Alison Jolly**

*Evolution's Rainbow* is written for professional biologists; pre-med and medical students; lesbians; gays; bi-, trans-, and intersexuals; and any other people who enjoy either sex or gender. The readership should, but undoubtedly won't, include the religious orthodox, who probably would not appreciate a transsexual professor of evolutionary biology quoting the Bible and the Koran.

Roughgarden begins with a review of sex and gender in animals and plants, structured to challenge current theories of sexual selection. She then describes the development of the embryo, the psychology of sex and gender diversity, and the treatment of sexually diverse people in ancient and modern cultures. She ends with policy recommendations for modern American society. The book is held together by her demand that we rethink our attitudes toward human diversity. In the calculus of reproductive success, homosexuals who divert mating energy to nonreproductive partners have always posed a problem to evolutionary theory, and people who choose to be celibate or sterile even more so. On the book's first page, Roughgarden suggests, "When scientific theory says something's wrong with so many people, perhaps the theory is wrong, not the people."

**Evolution's Rainbow**
**Diversity, Gender, and Sexuality in Nature and People**
*by Joan Roughgarden*
University of California Press, Berkeley, 2004. 480 pp. $27.50. ISBN 0-520-24073-1.

She describes the rainbow of sexuality in other species: hermaphrodites, sex changers, homosexual matings (known from more than 300 vertebrate species), species with three or more "genders," pairs of male swans who fledge more young than male-female pairs, and trios of bluegill sunfish (in which big territorial males court smaller male partners as well as females, and then the threesome spawns together). Roughgarden discards the idea that all these animals are "deceived" by mimicry of the other sex or "cuckolded" by sneaks. Often, she argues, they are cooperating in a wider social context than the simple reproductive pair.

She proposes that the theory of sexual selection should be replaced by one of "social selection," in which all the bonds between members of a society are recognized—including mating relationships that promote kin selection in the widest sense rather than individual reproduction. I agree that far too much of sexual selection theory has concentrated on species that mate at a lek (what Roughgarden calls a male red-light district), where females choose between posturing males who give them nothing but genes. Fascination with showy, competitive males and coy females has continued from Darwin down to present-day popularizers.

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