Beyond Reciprocity

Robert Costanza

BioScience, Vol. 48, No. 7. (Jul., 1998), pp. 564-565.

Stable URL:
http://links.jstor.org/sici?sici=0006-3568%28199807%2948%3A7%3C564%3ABR%3E2.0.CO%3B2-2

BioScience is currently published by American Institute of Biological Sciences.

nitely shape animals. By detailing the relationship between patterns of growth and evolutionary trends, he justifies how factors that are intrinsic to the organism must play a role in evolution. On the other hand, it must be said that not *all* intrinsic factors can be reduced to timing and rate of growth and that to do so is, in some sense, to simplify our view of organismal organization. That said, McNamara has detailed a number of engaging examples of heterochrony for the reader to pursue. In the end, as has been wisely pointed out, there is no disputing against hobbyhorses.

TERRI A. WILLIAMS
Department of Zoology
University of Texas
Austin, TX 78712

BEYOND RECIPROCITY

Cooperation among Animals: An Evolutionary Perspective. Lee Alan Dugatkin. Oxford University Press, NY, 1997. 216 pp., illus. $29.95 (ISBN 0-19-508622-8 paper).

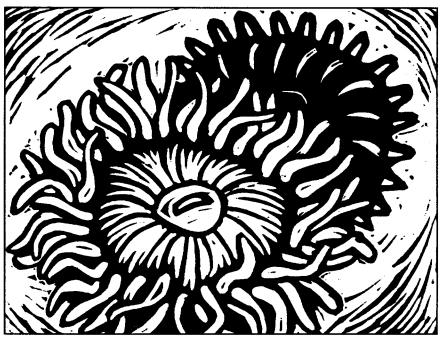
Cooperation among Animals, by biologist Lee Alan Dugatkin, marks a major step forward in our understanding of cooperative behavior. In an engaging, honest, and self-effacing style, Dugatkin summarizes the history of research on cooperative behavior in chapter 1, lays out a "grand theory" of cooperation in chapter 2, and then musters a prodigious amount of data and examples in fish, birds, mammals, and insects in chapters 3–7 to support it (the reference list, printed in small type, is 38 pages long). Chapter 8 summarizes the argument and presents prospects for the future.

Dugatkin's theory (see also Dugatkin 1997) is formulated in standard game theory format and is called the "cooperator's dilemma." It is an extension and expansion of the famous "prisoner's dilemma" to allow for three additional types of cooperative behavior in addition to the reciprocity that is usually studied with the prisoner's dilemma: kin selection, group selection, and byproduct mutualism.

The common element is the use of a two-player payoff matrix that summarizes the rewards (payoffs) to cooperative versus noncooperative behavior. The payoffs in the matrix are R (the reward for mutual cooperation), P (the payoff for mutual defection), T (the temptation to defect on a cooperating partner), and S (the sucker's payoff for cooperating when the partner defects). If $T > R > P > S$ and $2R > T + S$, then the game is a prisoner's dilemma. Cooperation in the prisoner's dilemma can evolve through reciprocity, but only if repeated encounters with the same individuals occur and if it is possible to remember what the other individual did during previous encounters (Axelrod and Hamilton 1981, Axelrod 1984).

Although the prisoner's dilemma and reciprocity have received an enormous amount of attention, the other three forms of cooperation that Dugatkin identifies have not. His "cooperator's dilemma" neatly generalizes the payoff matrix to allow the payoffs to take on other values and inequalities, and he notes the conditions under which all four forms of cooperation are likely to evolve. For example if $R > T \geq S > P$, then there is no "cost" to cooperate (because the reward for cooperation is greater than the temptation to defect or the payoff for mutual defection), and mutual cooperation would be the most attractive option, even in single encounters. This situation would be a case of byproduct mutualism. Examples include group hunting (as in yellowtail mackerel and Harris' hawks) and allogrooming (as in impala and chimps).

Byproduct mutualism may very well be the most common and important path to cooperation, but it has received only scant attention in the literature. Theoretical work in biology, Dugatkin notes, is heavily skewed toward models of reciprocity, and the huge literature about cooperation in fields other than biology (e.g., economics, political science, and other social sciences) is even more skewed. Why? asks Dugatkin. One reason may be that reciprocity, although a more difficult path to cooperation, requires "scorekeeping," a feature that may appeal to human scorekeeping researchers. Being the more difficult path to explain, reciprocity may also appeal to researchers' sense of challenge. In any event, Dugatkin argues for righting the imbalance and giving the other three paths to cooperation their rightful due.



Thus, Dugatkin also explores the conditions for kin selection and group selection. Although the existence of kin selection is widely accepted these days, group selection has only recently been revived after a period of near total rejection (Wilson 1990, Wilson and Sober 1994). This "new" group selection is more accurately referred to as "trait group selection." Group-selected behavior requires broadening the scope of interactions to include the indirect effects of an individual's behavior on the productivity of its local subpopulation or "trait group." The difference between this "new" group selection and "old" group selection is that rather than proposing the differential extinction of whole subpopulations as the main selection mechanism, it proposes differential productivity between subgroups with different proportions of cooperators and defectors. Cooperation evolves when the increased productivity of groups with many cooperators outweighs the within-group benefit to being selfish (Dugatkin and Reeve 1993).

The problem with all these theoretical arguments, as Dugatkin hastens to point out, is that actual measurements of payoff matrices for use in testing the theory are few and far between. He acknowledges that most of the examples that he is able to cite are anecdotal at best and that "the lack of data on payoff matrix entries is often the first and strongest critique" (p. 165). He notes that "Clements and Stephens' (1995) work on byproduct mutualism in foraging blue jays is the only example in this entire book in which we know the exact values associated with a game" (p. 165). Nevertheless,

he notes that knowledge of *inequalities* among the payoff matrix entries is often sufficient to test the theory and that work is progressing rapidly in measuring payoffs, at least in controlled experimental setups. Another challenge for the future is to bring in the spatial dimension of cooperative behavior. For example, Nowak and May (1992) have shown that cooperation can evolve in a spatial prisoner's dilemma even without reciprocity.

In any event, our understanding of cooperative behavior in animals is progressing rapidly, and getting past the hang-up on reciprocity should help us to achieve a more balanced and complete picture. If only academics could learn to cooperate as well as the rest of the animal kingdom apparently does, we might make even faster progress.

ROBERT COSTANZA
Center for Environmental Science, Biology Department, and Institute for Ecological Economics
University of Maryland
Solomons, MD 20688-0038

References cited

Axelrod R. 1984. The Evolution of Cooperation. New York: Basic Books.

Axelrod R, Hamilton WD. 1981. The evolution of cooperation. Science 211: 1390–1396.

Clements KC, Stephens DW. 1995. Testing models of animal cooperation: Feeding bluejays cooperate mutualistically, but defect in a massively iterated Prisoner's Dilemma. Animal Behavior 50: 527–535.

Dugatkin LA. 1997. The evolution of cooperation: Four paths to the evolution and maintenance of cooperative behavior. BioScience 47: 355–362.

Dugatkin LA, Reeve HK. 1993. Behavioral ecology and the "levels of selection": Dissolving the group selection controversy. Advances in the Study of Behavior 23: 101–133.

Nowak M, May RM. 1992. Evolutionary games and spatial chaos. Nature 359: 826–829.

Wilson DS. 1990. Weak altruism, strong group selection. Oikos 59: 135–140.

Wilson DS, Sober E. 1994. Re-introducing group selection to the human behavioral sciences. Behavioral and Brain Sciences 17: 585–654.

PUBLISHING NEWS

The Missouri Botanical Garden Press recently published *Flora of the Venezuelan Guayana: Caesalpiniaceae-Ericaceae*. Edited by Paul E. Berry, Bruce K. Holst, and Kay Yatskievych, this volume is the fourth in a set of nine that is to be the first full scientific account of the plants of this botanically rich and geologically ancient part of South America. *Flora of the Venezuelan Guayana* is available for $67.95. To order, contact: Missouri Botanical Garden, MGB Press Orders, 4344 Shaw Blvd., St. Louis, MO 63110; Tel: 314/577-9534; fax: 314/577-9591; e-mail: mgbpress@mobot.org; Web site: http://www.mobot.org/MOBOT/research/scipubs/title.html.

NEW TITLES

A Field Guide to the Invisible. W. Biddle. Henry Holt and Company, New York, 1998. 208 pp., illus. $23.00 (cloth).

Genetics Manual: Current Theory, Concepts, Terms. G. P. Rédei. World Scientific Publishing, River Edge, NJ, 1998. 1142 pp., illus. $78.00 (cloth).

A Guide to the Polyamines. S. S. Cohen. Oxford University Press, New York, 1998. 595 pp., illus. $160.00 (cloth).

Hormones and Growth Factors in Development and Neoplasia. R. B. Dickson and D. S. Salomon. Wiley, New York, 1998. 461 pp., illus. $125.00 (cloth).

Influential Passengers: Inherited Microorganisms and Arthropod Reproduction. S. L. O'Neill, A. A. Hoffmann, and J. H. Werren, eds. Oxford University, New York, 1997. 214 pp., illus. $95.00 (cloth).

Mood Genes: Hunting for Origins of Mania and Depression. S. H. Barondes. W. H. Freeman and Company, New York, 1998. 209 pp., illus. $24.95 (cloth).

Other Worlds: The Search for Life in the Universe. M. D. Lemonick. Simon & Schuster, New York, 1998. 272 pp., illus. $25.00 (cloth).

The Phytogeography of Northern Europe: British Isles, Fennoscandia and Adjacent Areas. E. Dahl. Cambridge University Press, New York, 1998. 295 pp., illus. $95.00 (cloth).

Plant Cold Hardiness: Molecular Biology, Biochemistry and Physiology. P. H. Li and T. H. H. Chen, eds. Plenum Publishing. New York. 1998. 368 pp., illus. $125.00 (cloth).

Unto Others: The Evolution and Psychology of Unselfish Behavior. E. Sober and D. S. Wilson. Harvard University Press, Cambridge, MA, 1998. 394 pp., illus. $29.95 (cloth).

The World of the Harvester Ants. S. W. Taber. Texas A&M University Press, College Station, TX, 1998. 232 pp., illus. $34.95 (cloth).

Wildlife of the Tibetan Steppe. G. B. Schaller. University of Chicago Press, Chicago, 1998. 384 pp., illus. $55.00 (cloth).

NOW IN PAPERBACK

Agroforestry for Soil Management. A. Young. Oxford University Press, New York. 1998. 320 pp., illus. $45.00 (paper).

Complimentary & Alternative Medicine. Legal Boundaries and Regulatory Perspectives. M. H. Cohen. Johns Hopkins University Press, Baltimore, MD, 1998. 180 pp. $16.95 (paper).

Darwin's Dreampond: Drama in Lake Victoria. T. Goldschmidt. MIT Press, Cambridge, MA, 1998. 280 pp., illus. $15.00 (paper).

A Field Guide to Common South Texas Shrubs. R. B. Taylor, J. Rutledge and J. G. Herrera. University of Texas Press, Austin, TX, 1997. 106 pp., illus. $19.95 (paper).

Financing Change: The Financial Community, Eco-Efficiency, and Sustainable Development. S. Schmidheiny and F. J. L. Zorraquin. MIT Press, Cambridge, MA, 1998. 209 pp. $15.00 (paper).

The Florida Panther: Life and Death of a Vanishing Carnivore. D. S. Maehr. Island Press, Washington, DC, 1998. 320 pp., illus. $19.95 (paper).

Global Environment Outlook: For Life on Earth. United Nations Environment Programme. Oxford University Press, New York, 1997. 264 pp., illus. $25.95 (paper).

Global Governance: Drawing Insights from the Environmental Experience. O. R. Young, ed. MIT Press, Cambridge, MA, 1998. 344 pp. $40.00 (paper).

Human Well-Being and Economic Goals. F. Ackerman, D. Kiron, N. R. Goodwin, J. M. Harris, and K. Gallagher, eds. Island Press, Washington, DC, 1998. 395 pp., illus. $30.00 (paper).

Improving Nature? The Science and Ethics of Genetic Engineering. M. J. Reiss and R. Straughan. Cambridge University Press, New York, 1998. 288 pp., illus. $15.95 (paper).

State of the World: 1998. L. Brown, C. Flavin, J. Abramovitz, C. Bright, S. Dunn, G. Gardner, A. McGinn, J. Mitchell, M. Renner, D. Roodman, L. Starke and J. Tuxill. Worldwatch Institute, Washington, DC, 1998. 251 pp., illus. $13.95 (paper). ❑