

they build on insights from psychology and incorporate learning, adaptation, and so forth.

Unfortunately, much of evolutionary game theory is solely concerned with foundational questions, e.g., how to characterize Nash equilibrium (or its refinements) in terms of adaptive mechanisms. Much less work has focused on using the proposed dynamic models directly to explain social phenomena. Given, on the one hand, the computational difficulties to doing that and, on the other hand, the rich modeling capabilities offered by agent-based models, there seems to be ample room for collaboration and convergence. Perhaps such efforts offer a more fruitful direction than the ongoing argument over which approach is right.

Epstein's book is a concise and well-articulated defense of agent-based modeling. *Generative Social Science* is essential reading for anyone seriously interested in the foundations and the practice of agent-based modeling. In my view it does not settle the questions, but stating them clearly and providing a clear and provocative argument is no minor achievement.

References

1. T. C. Schelling, *Micromotives and Macrobehavior* (Norton, New York, 1978).
2. T. Hobbes, *The Elements of Law Natural and Politic* (1640); www.efm.bris.ac.uk/het/hobbes/elelaw.

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EVOLUTION AND BEHAVIOR

Simple Maths for a Perplexing World

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Charles Darwin famously remarked that those versed well in mathematics are endowed with something akin to an extra sense. In the past half century, mathematics has brought a great deal of insight into evolutionary biology, and perhaps for this reason hoards of mathematicians and physicists flock to biology to apply their insight. The depth and range of topics dealt with in Richard McElreath and Robert Boyd's *Mathematical Models of Social Evolution* keenly demonstrate how far that extra sense can bring us.

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The book begins with the analogy that mathematics is like Latin: everyone knows a few words, but very few people can understand a sentence. The analogy is a good one, as mathematics takes a back seat in most biology programs. McElreath and Boyd (anthropologists at, respectively, the University of California, Davis, and the University of California, Los Angeles) hope for nothing less than a reformation in evolutionary biology, and like Martin Luther (who translated the Bible from Latin into the vernacular), they succeed very well in conveying their ideas to the perplexed. Simply flicking through the book without reading the details is enough to panic anyone with even a slight phobia of equations: the book is packed with squiggles, little letters, and strange-looking symbols. Taking the plunge, however, reveals that the authors have explained each step of the chosen models as clearly as possible. These widely used models are elegant in their mathematical simplicity, and at times the prose reads like a bedtime story, prompting the reader to think "how simple!"

Each chapter is followed by a guide to the relevant literature, and a detailed appendix covers some of the most useful techniques in mathematical biology. Classic topics such as animal conflict, sex allocation, and dispersal are discussed. Disappointingly, the authors neglect a few well-used approaches, including simulations (which they dismiss from the start), standard optimization theory, and dynamic programming. Those interested in such tools will find Hanna Kokko's recent book (*J*) helpful.

Much of the mathematical theory of social evolution theory stems from the work of W. D. Hamilton, and his results feature prominently in the book. The two chapters devoted to cooperation and reciprocity introduce both game theoretical and inclusive fitness techniques for approaching these problems. These chapters offer a comprehensive introduction to what increasingly seems a mammoth field on its own; clearly, the tool box that the authors use in their day-to-day research is immense. Hamilton (2) noted that altruistic behaviors could evolve if the cost (c) that an altruist paid was less than the benefit of the recipient, weighted by the relatedness coefficient (r): $c < rb$, known as Hamilton's rule. One long-standing issue in the field of social evolution concerns what role group selection (where an individual's fitness depends on the success of the group) plays in the evolution of altruism—a question recently addressed in (3, 4). In their

chapter on selection among groups, the authors use an elegant model to show that both kin selection and group selection approaches to altruism yield Hamilton's rule. As they remark: "There is only one world out there. It would be bad if changing the way we did the accounting of genes changed the answer."

One of the most interesting topics McElreath and Boyd cover is social learning (learning from observing and copying others). Many animals have the ability to copy each other; thus, behaviors can be transmitted by learning from other animals as well as by genes. In the introductory chapter, the authors discuss a simple model that allows one to calculate the frequency of copied behaviors when animals estimate payoffs to others in deciding whether to imitate another individual and which behavior to copy. In their chapter on animal communication, the authors con-

sider such cultural inheritance in a fictitious species that inhabits a changing environment. Using a model of gene-culture coevolution (which allows both genes and culturally inherited traits to evolve), they then examine the conditions under which social learning can evolve. They show that for more predictable environments, social learning is favored over individual learning (learning purely from one's own

experience). The field of cultural evolution is still fertile ground, and the ideas presented in the authors' discussion of social learning will spur many a biologist to think more about the role of cultural transmission in evolutionary change.

Mathematical Models of Social Evolution will no doubt reward psychologists, sociologists, and economists interested in evolutionary theory. Anyone desiring a thorough, yet down-to-Earth, introduction to modeling in social evolution couldn't do much better than to read this book. Using little more than high school mathematics, McElreath and Boyd show how one can take a big step toward understanding many perplexing evolutionary processes.

References

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