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Book reviews

Laying bare the machinery-Mathematical models of social evolution: a guide for the perplexed.
McElreath R., Boyd R. (2007, Spring: Chicago, IL; University of Chicago Press)
ISBN: 978-0-226-55826-4 (432 pp, $62.50)

More and more researchers in such areas as social and cognitive psychology, sociology, and anthropology are beginning to attend to ultimate (evolutionary) explanations and their more traditional proximate concerns when they frame their hypotheses. Most readers of this journal, like this author, will probably view this as an entirely desirable and long overdue development. Darwinian evolutionary theory is, after all, the only possible framework for transforming the balkanized and parochial little sets of partial generalizations about human behavior that constitute the human sciences into a unified and deeply explanatory field. Thus, the more people start taking the evolutionary dimension seriously, the better.

Like marriage, however, it is going to take some hard work at the beginning. Subject areas such as social and cognitive psychology (unlike economics) have no tradition of strong a priori theorizing. Instead, "theory" in these areas often refers to inductively generated generalizations or typologies of behavior. More particularly, they have almost no tradition of mathematical analysis or modeling. The Darwinian motor on which they are now seeking to harness their explanatory program is the strategic ESS (evolutionarily stable strategy) thinking of Fisher, Hamilton, Maynard-Smith, and others. All of the main ideas of this literature were derived either through mathematical modeling or from a priori verbal reasoning and later shown to be viable using mathematical models. Either way, mathematical modeling—far more than induction from data—is at the heart of the beliefs that modern evolutionary theorists hold.

This can lead to some cultural differences when social scientists join the evolutionary enterprise, most notably in what counts as theory and explanation. It also leads to an important informational asymmetry. Most psychologists and social scientists do not have the mathematical toolkit needed to understand how the theoretical postulates of modern Darwinism have been arrived at. It is as if, as Richard McElreath and Robert Boyd point out in their preface, the liturgy were in Latin such that ordinary devotees could not really access its meaning and must thus rely on a small priestly caste to translate its implications for them. The evolutionary psychology instructor can often find himself or herself having to say, "Believe me, Alan Grafen showed it works, you have to take my word for it, as I in turn took Richard Dawkins' word." This might be compared with the position of the medieval scholastic philosophers who could allegedly terminate any skepticism by saying, "Aristotle hath said it." In this book, McElreath and Boyd set out to equip anyone who wants it with the basic toolkit that he or she will need to read the liturgy in the original.

Before turning to what the book contains, it is worth briefly considering whether it matters that most empiricists in the field of the human sciences are not fluent in theory. Perhaps it does not. As long as theoreticians can spell out their more testable predictions for the data collectors to go and design studies on, surely, it is a reasonable division of labor and there is no point in a social psychologist trying to understand, say, the mathematics of game theory.

McElreath and Boyd clearly do not think so and make a convincing case for their view. The more one understands the underlying theory, the more nuanced one can be with one's predictions. It is all too easy to perpetuate loosely specified ideas (group selection can never be important, behaviors that benefit kin will always spread as long as $rb>c$, reciprocal altruism persists as long as the parties have a high probability of repeat interaction, signals can only be honest if they are costly, etc.) when, in fact, things are not always so. It makes a great deal of difference what the population structure and context are. One of the strongest lessons from mathematical modeling is that almost anything can evolve under the right conditions. The interest is in seeing what those conditions are and how the biology and ecology of particular species might or might not meet them. Being illiterate in theory means accepting generalizations from models without the tools to question whether those models apply to the system one is working on. Another hazard is seeing various ideas that have been discussed in the literature (multilevel vs. gene-level selection, reciprocity and kin selection, good genes vs. runaway models of sexual selection, etc.) as alternatives when a deeper understanding of theory shows that they are all special cases of much more general principles and not necessarily mutually exclusive. Above all, Darwinian ESS theory is less a set of generalizations than a way of thinking about the world (asking *why*, not *how*), and you do not get that way of thinking without understanding something of how the models actually work.

The book is actually rather broader than its title implies, because to look at models of social evolution, the work

must consider the basic underlying models of evolutionary genetics. Thus, there are good treatments of how to conceptualize fitness, model allele frequency change, and derive equilibria and examine their stability. McElreath and Boyd clearly see George Price's covariance approach to evolution and selection as fundamental. They use it not only in the context in which it is most often discussed, the derivation of Hamilton's rule, but also in numerous other places. Indeed, the most impressive thing to be taken from the book is how, at a sufficiently abstract level, the principles underlying areas as apparently diverse as kin selection, cooperation, signaling, and sex allocation are largely the same.

The authors deliberately intersperse the introduction of the general mathematical heavy machinery with case studies on topics that are of interest to students of evolution and human behavior. The topics covered include conflict resolution, kin selection, reciprocity and collective action, signaling, the evolution of social learning, levels of selection, sex allocation, and sexual selection. Along the way, the more frequent misunderstandings of evolutionary ideas are very patiently exposed. For example, there is a nice treatment of why the coefficient of relatedness is not the probability of two individuals sharing the same allele at a locus. After all, many human alleles are at fixation, and this does not mean we all have r=1. Similarly, we are shown how Hamilton's rule relies on selection not being too strong and thus avoids the problem of the kin-directed self-sacrifice mutant allele instantly driving itself extinct.

All in all, this is a fantastically stimulating and useful book for anyone who wants to think about a topic of study from a Darwinian point of view. Understanding the principles within it can help move a graduate student or researcher from being someone who waits patiently at the outlet of the evolutionary theory black box to someone who is comfortable playing around with the machinery itself. The book is about as accessible as it is possible for it to be, but it is, of course, very mathematical. The chapter on sexual selection in particular is quite hard going. However, there is surprisingly little that is too challenging for anyone comfortable with basic algebra and calculus. The style is—if this makes sense for a book of mathematics—quite informal, going directly for the main conceptual principles. Problems and work solutions are also provided.

If we are to produce a fruitful iterative cross-talk between theory and data in the study of evolution and human behavior, then we should all try to get on top of the principles elaborated here. Whether everyone will is another matter. Stephen Hawking commented in his book, *A Brief History of Time*, that every equation in a book halves its potential readership. If true, this would leave *Mathematical Models of Social Evolution: A Guide for the Perplexed* largely unread. However, the payoff for the field is too great for this to happen, and I hope this book becomes a standard reading for graduate students of evolution and human behavior.

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Are readers of *Evolution and Human Behavior* interesting people? A review of Hanna Kokko's *Modelling for Field Biologists and Other Interesting People.*

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> "Any sufficiently advanced technology is indistinguishable from magic." Arthur C. Clarke's third law

Utter the word "model" in certain academic circles and you are sure to generate controversy. Some complain that, while useful, the mathematics are beyond them. Others, with or without confidence in their math abilities, assert that models do not tell you anything you did not know or could not have already known. Still others believe models to be useful, but it is, alas, too late for them to begin the training in these arcane skills.

As few researchers are trained in a diversity of modeling techniques, building models often seems magical. Nothing could be further from the truth. Just like well-designed experiments, carefully constructed models seek to reveal the causal relationships between variables, all else being equal. While experiments seek to know if something occurs in nature, models serve as existence proofs, putting verbal logic to a more precise test. We believe that it is crucial for evolutionary behavioral scientists to add this kind of modeling to their methodological skills set. Even if one's goal is not to make models, one should still be an educated consumer of them.

Unfortunately, learning to decipher and develop models can be difficult. The problem is finding the right guide. In addition to publishing important theoretical contributions, such as unifying Fisher's runaway hypothesis and Zahavi's good genes model (Kokko, Brooks, McNamara, & Houston, 2002), Kokko has written an excellent accessible introductory text on ecological and evolutionary modeling. As the title suggests, this book is intended for those with "no hands-on experience with mathematical modelling so far" (p. ix).

1. A model of the book

Kokko's philosophy is to build models as simply as possible. She rightfully concedes that reality is a tangle of causes and effects where everything interacts with everything else. Right away, she discourages us from building