EVOLUTION

O Brave New World with Such Games

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Crucial contest. Black grouse (*Tetrao tetrix*) clashing at Finnish lek.

A stag might fight to death over a territory or concede it uncontested to another. Neighboring trees invest varying amounts of energy into growth, with the tallest blocking sunlight to others. Viruses infecting a common cell can either make all proteins required for their reproduction or free ride on those made by others. How does evolution shape the strategic phenotype of organisms in life-and-death contests?

Such questions fall within the domain of evolutionary game theory, a field that combines strategic concerns with the fundamental principles of evolution. A game is a simple way to represent interactions. Players choose from a set of possible strategies; for example, fight or retreat, cooperate or defect. The results are recorded as payoffs received by each player. The basic idea of evolutionary game theory is to link payoff to reproductive success (*1*). Thus, a successful strategy will increase in abundance over generations as it is successively transmitted from parent to offspring. Evolutionary game theory applies whenever fitness depends on the phenotypes or actions of others; the fitness landscape changes as the population explores it (*2*). The resulting evolutionary dynamics can lead to dominance of a single strategy, coexistence of multiple strategies, periodic cycling, or even chaos (*3*).

In its first decades, evolutionary game theory focused primarily on notions of evolutionary stability and deterministic dynamics. Previous textbooks (*3–6*) concentrated on these early themes. However, the scope of evolutionary game theory is rapidly expanding—both in terms of the range of situations considered and the variety of underlying models of evolution. Mark Broom and Jan Rychtář's *Game-Theoretical Models in Biology* provides a comprehensive, up-to-date introduction that uniquely blends mathematical clarity and biological intuition.

Game-Theoretical Models in Biology

by Mark Broom and Jan Rychtář

Chapman and Hall/CRC Press, Boca Raton, FL, 2013. 520 pp. $79.95, £39.99. ISBN 9781439853214.

The first half explores the many ways that the concepts "game" and "evolution" can be realized. Moving beyond the traditional focus on matrix games, Broom and Rychtárˇ (mathematicians at City University, London, and the University of North Carolina at Greensboro, respectively) explore nonlinear and asymmetric games, games among many players, games with sequential moves, and games that change with players' ages and other variables. They discuss not only evolution in terms of competition among existing strategies but also long-term evolution through successive trait substitutions. The authors also examine the effects of population size and structure, providing an entry point into one of the most active and exciting new directions in the field.

The second half brings to life the mathematical frameworks introduced earlier, focusing on specific investigations of important biological phenomena. Through detailed exposition and modeling of conflicts that arise in the contexts of group living, mating, foraging, and predation, the authors illuminate not only the behaviors that emerge in these particular contexts but also the process of matching mathematical framework to biological reality, a critical skill for aspiring evolutionary theorists. One especially interesting analysis considers a sperm-allocation dilemma: males must produce the amount that maximizes their reproductive chances, given that each female may mate with multiple males.

One chapter concerns the evolution of cooperation, a topic of great interest in biology, psychology, economics, and philosophy. A controversy in this field exists over kin selection, by which cooperation can spread if the benefits go primarily to genetic relatives. In some simplified models, this idea can be formulated as Hamilton's rule. In dispute is whether kin selection is a universal explanation for cooperation or merely one mechanism among several (*7*). This seemingly straightforward question has become clouded for two reasons. First, some researchers apply the term "kin selection" to any situation in which there is association (genetic or not) among like phenotypes, thus vastly stretching its meaning. Second, some use linear regression to rewrite frequency changes so that Hamilton's rule appears to be satisfied, regardless of the underlying biological reasons for change. In contrast, Broom and Rychtář offer a refreshingly clear exposition of kin selection, using a simple model with direct biological interpretation. They present this alongside other, distinct, mechanisms for cooperation such as direct and indirect reciprocity, avoiding the confusion that muddles much of the literature on this topic.

Legend has it that John Maynard Smith invented the concept of evolutionary stability after quitting a technical account on game theory a few pages before he would have encountered the Nash equilibrium. Students of evolutionary game theory, however, would do well to read *Game-Theoretical Models in Biology* all the way to the finish line. This engaging primer demonstrates that there is no tension between mathematical elegance and biological fidelity: both are needed to further our understanding of evolution.

References

1. J. Maynard Smith, G. R. Price, *Nature* **246**, 15 (1973).
2. M. A. Nowak, K. Sigmund, *Science* **303**, 793 (2004).
3. J. Hofbauer, K. Sigmund, *Evolutionary Games and Population Dynamics* (Cambridge Univ. Press, Cambridge, 1998).
4. J. Maynard Smith, *Evolution and the Theory of Games* (Cambridge Univ. Press, Cambridge, 1982).
5. J. W. Weibull, *Evolutionary Game Theory* (MIT Press, Cambridge, MA, 1995).
6. K. Sigmund, *The Calculus of Selfishness* (Princeton Univ. Press, Princeton, NJ, 2010).
7. M. A. Nowak, *Science* **314**, 1560 (2006).

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