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Principles of Social Evolution: The Grandeur of Inclusive Fitness
Book Review

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Principles of Social Evolution, by Andrew F. G. Bourke. Oxford University Press, 2011, 267 pp., US$ 55. ISBN 978-0-19-923116-4 (Paperback)

Introduction

Principles of Social Evolution by Andrew Bourke is an ambitious book. The author sets out to show how inclusive fitness theory (a more accurate label than "kin selection") provides common principles of social evolution that apply at each step in all the major evolutionary transitions—including the evolution of eukaryotic cells, sexual reproduction, multicellularity, eusociality, and interspecific mutualism. In the process, the book explores a range of phenomena of crucial importance to behavioral biologists and psychologists: the dynamics of group formation, the emergence and resolution of social conflict, the ways in which groups limit exploitation by selfish members, and many more. As noted by the author, this approach promises to bring conceptual unification to "an immense range of superficially different phenomena in different taxa" (p. 5). On another level, the book can be read as a vigorous defense of inclusive fitness theory as a truly general theory of social evolution.

Chapter two introduces the reader to inclusive fitness theory, from the basics of Hamilton's rule to more advanced topics such as intragenomic conflict, green-beard effects, and the effects of dispersal on the evolution of altruism. Also, the chapter reviews and addresses a number of common criticisms and objections to the theory. In my opinion, this chapter alone is worth the price of the book; its clarity and accessibility—the math is kept to a minimum—make it an excellent teaching resource for courses on behavioral evolution (see also West et al., 2011 for a human-centered overview).

In chapter three, Bourke sets the stage for interpreting the major evolutionary transitions in light of inclusive fitness theory, building on Queller's (2000) distinction between "fraternal" transitions (associations of relatives, for example cells in multicellular individuals) and "egalitarian" transitions (associations of non-relatives, for example nucleus and organelles in eukaryotic cells). The central theme of the chapter is conflict between individual entities and how it can be resolved, allowing lower-level entities to group together and eventually transform into a new kind of higher-level individual. In particular, the chapter discusses

the role of relatedness in determining both the intensity of conflict and the range of potential resolution tactics.

The next three chapters explore the logic of social evolution by segmenting transitions to higher-level individuality into three steps: group formation (chapter four), maintenance (chapter five), and transformation (chapter six). Each chapter examines the relevant step in detail and discusses the main evolutionary challenges faced by biological entities as they move toward a social transition. Chapter four (group formation) is relatively straightforward but informative and well-organized. The distinction between genetic, ecological, and synergistic factors favoring group formation drives home the point that inclusive fitness is not just about relatedness, and thoroughly illustrates how direct costs and benefits play a fundamental role in the overall economy of Hamilton's rule.

Readers with an interest in social behavior will find chapter five (group maintenance) especially stimulating, as it deals with the crucial problem of how exploitation from external and internal agents can be successfully limited once a group is formed. The chapter covers a broad range of topics including recognition of self versus non-self, negative frequency-dependence as a limit to exploitation, and the variety of coercion strategies found across levels of biological organization, from mitochondria to insect colonies. The strength of this chapter lies in the way these apparently disparate topics are brought together and reconnected to the fundamental logic of inclusive fitness.

Chapter six (group transformation) contrasts simple and complex social groups and discusses how group size and complexity may be causally and functionally related. Admittedly, this chapter is more speculative and based on sparser evidence than the rest of the book. Still, it introduces a wealth of stimulating but relatively unexplored ideas and theories, some of which may be unfamiliar even to expert readers. In particular, Bourke provides a fresh perspective on reproductive and non-reproductive division of labor—a topic with many potential implications for the evolution of human societies. Chapter seven sums up the previous chapters, summarizes the principles discussed in the book, and concludes by speculating on future evolutionary trends—what will be the next major transition?

In summary, *Principles of Social Evolution* is a remarkable book, written in an engaging yet unassuming style and filled with fascinating examples and case studies. Its brevity (267 pages including references) testifies to the author's ability to synthesize complex arguments while retaining clarity and breadth of scope. Of course, only time will tell whether Bourke has succeeded in his ambitious synthesis. Proponents of multilevel selection and critics of inclusive fitness theory may find the book irritating because of the short shrift it gives to alternative approaches. While I share Bourke's theoretical stance, I believe that the book would have benefited from a more explicit discussion of how inclusive fitness and multilevel selection relate in practice (e.g., Lehmann et al. 2007; Marshall 2011). Even so, the book should prove useful to critics as a concise, clearly articulated statement of the biological "theory of everything" from an inclusive fitness perspective. Another minor limitation of the book concerns the treatment of population viscosity (i.e., limited dispersal of offspring). The take-home message of the relevant section seems to be that, in general, limited dispersal hinders the evolution of altruism (p.47). While the author later qualifies this statement (p. 49), readers may easily overlook the qualifications and get away with a simplistic view of this important issue. To correct this imbalance one may wish to consult Lehmann et al. (2008), as well as more recent work by Van Dyken and Wade (2012a, 2012b).

For those with a background in evolutionary biology, *Principles of Social Evolution* will help clarify familiar concepts and provide insight in how those concepts relate to one another and to the bigger picture of social evolution. Readers whose primary interest is in human behavior should not be deterred by the eclectic content of the book. The power of inclusive fitness theory lies in its generality—and in the surprising

analogies it suggests between apparently disparate biological phenomena at widely different scales. This is why, as deftly put by the author (p. 71), inclusive fitness theory is "an orthodoxy that the open-minded can feel at home in."

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