Book Review

Inclusive Fitness
101: Math Not
RequiredUlrich R. Ernst^{1,*}

Inclusive fitness theory delivers a clever solution to the problem of altruism, especially the case of sterile worker castes in social insects. The idea behind the inclusive fitness theory is straight forward and contemporary: if you can somehow outsource reproduction, then you may reduce (or stop) personal reproduction. You do not have to copy your genes yourself if somebody else can do it for you. Just who this somebody else should be, and how much you should be willing to pay for it, was famously derived by Hamilton [1,2]. It can be captured in an elegant and simple way, widely known as Hamilton's rule: $rb - c > 0$; that is, to be selected by natural selection, the *benefit* of helping a *related* individual must outweigh the *costs* to personal reproduction. This insight spurred

much research in the field of behavioral ecology and led to an overarching theory of social evolution. Alas, the simplicity of this popular form of Hamilton's rule comes at a price: it requires several assumptions (which are not likely to be met) and, therefore, is not general. In fact, the way I presented it here is likely to be wrong in many cases. Indeed, for many experimental biologists, the terms and conditions that apply can be a challenge to fully understand. Of course, there are more general forms of Hamilton's rule, but most of them are only known to theoreticians, and the mathematics behind them may be daunting for many hands-on biologists. This is where Marshall aims to help with *Social Evolution and Inclusive Fitness Theory* by explaining the formulas in an easy-to-follow way, and showing that Hamilton's rule is generally applicable. The first task is partly accomplished by banning most of what are, for some biologists, frightening formulas and derivations to the extensive notes (more than a quarter of the main text). Given that equations in a text, but not in the appendix, may repel or reduce the number of nontheoretician readers [3], this was arguably a judicious strategy. By contrast, if the reader's main goal was to understand the math, this forces them to go back and forth frequently. Here, some boxes in the main text might have been a better option. In any case, while some of the derivations and equations still require some thinking, even the less numerically inclined readers can experience pleasure in finally grasping some of the ways the formulas work, such as why some terms cancel out.

The other target of showing the generality of inclusive fitness theory may not have been met entirely. Moreover, on several occasions, Marshall acknowledges shortcomings of some of the methods used, such as the fact that the Price equation is often not dynamically sufficient. That is, it cannot be applied repeatedly to several generations. However, this is a problem of the specific model at hand, and the

strength and merit of Marshall's review is to remind his readers of the difference between the mathematical tools (e.g., replicator dynamics) versus concepts (i.e., inclusive fitness) [4]. In other words, Marshall argues convincingly that inclusive fitness is a general concept, and that specific models require specific methods that render them less general, although he does not provide definite proof for the former.

Some topics do require a more detailed explanation for the inexperienced readers making their first steps into the field of social evolution. For instance, the discussion of relatedness may be bewildering at times, with negative relatedness only mentioned *en passant*, and the interpretation of altruism between species is confusing (where some argue that relatedness equals one, even though no genes are shared). Will this help to settle the dispute about the validity of inclusive fitness theory? I doubt it, because, by design, this primer of inclusive fitness theory only touches on the more accessible mathematical models, and it becomes clear that, even when one can follow the derivation of various formulations of Hamilton's rule, this is not sufficient to judge the validity of these or alternative explanations for altruism.

The reader interested in constructing their own models will likely want to access more advanced books (e.g., [5,6]). Owing to the focus of the book on the mathematical roots, the biological aspects of social evolution are also mentioned only rather briefly, and other works will be more appealing in that respect (e.g., [7]). However, this volume is a helpful introduction to inclusive fitness theory for those interested in starting to dig more into the theoretical foundations of social evolution, because it requires relatively moderate mathematical skills. Recognizing the diversity of modeling approaches and understanding their assumptions, advantages, and limitations will help to

advance the field of social evolution as a whole.

Social Evolution and Inclusive Fitness Theory: An

Introduction by James A.R. Marshall. Princeton University Press, 2015. US\$39.95/£27.95, hbk (216 pages) ISBN: 9780691161563

¹Laboratory of Functional Genomics and Proteomics, Department of Biology, KU Leuven, Naamsestraat 59, bus 2465, 3000 Leuven, Belgium

*Correspondence: uli.ernst@bio.kuleuven.be (U.R. Ernst).
<http://dx.doi.org/10.1016/j.tree.2016.01.001>

References

1. Hamilton, W.D. (1964) Genetical evolution of social behaviour 1. *J. Theor. Biol.* 7, 1–16
2. Hamilton, W.D. (1964) Genetical evolution of social behaviour 2. *J. Theor. Biol.* 7, 17–52
3. Fawcett, T.W. and Higginson, A.D. (2012) Heavy use of equations impedes communication among biologists. *Proc. Natl. Acad. Sci. U.S.A.* 109, 11735–11739
4. Gardner, A. *et al.* (2011) The genetical theory of kin selection. *J. Evol. Biol.* 24, 1020–1043
5. Frank, S.A. (1998) *Foundations of Social Evolution*, Princeton University Press
6. McElreath, R. and Boyd, R. (2007) *Mathematical Models of Social Evolution: A Guide for the Perplexed*, University of Chicago Press
7. Bourke, A.F.G. (2011) *Principles of Social Evolution*, Oxford University Press