GfÖ
GfÖ Ecological Society of Germany, Austria and Switzerland
Basic and Applied Ecology 54 (2021) 50–51
www.elsevier.com/locate/baae
Basic and Applied Ecology

BOOK REVIEW

Game Theory in Biology: Concepts and Frontiers, J. M. McNamara, O. Leimar, Oxford University Press (2020). 352pp., £70.00 (Hardback), £34.99 (Paperback), ISBN: 9780198815778 (Hardback), 9780198815785 (Paperback).

Evolutionary game theory owes its conception almost entirely to John Maynard Smith's work in the 1970s. It takes a village to raise a theory, though, and few have contributed as much to the field's maturation as John McNamara and Olof Leimar. I was consequently delighted to get my hands on their new book, which distils over four decades of insights into a neat three hundred pages.

This is not My First Evolutionary Game Theory. Some prior familiarity with evolutionary biology and the theory of games is essential to understanding both the book's mathematical arguments and their reasons for existing. Empirical biologists seeking a gentle introduction to modelling evolution would be better off elsewhere. (My recommendation is Kokko (2007)). On the other hand, mathematically mature readers – especially those dipping their first toes into evolutionary biology – may feel frustrated by the scarcity of formal definitions and proofs. Such readers might want to first prepare their minds with a more structured work. (An excellent springboard is Broom & Rychtář (2013)).

For the people it is presumably meant for – behavioural ecologists and their kin, whether theoretically or empirically oriented – this book is an absolute gem. It is insightful and remarkably readable, imparting the logical flavour of complex arguments without bogging the reader down in unnecessary details. A particular strength is the authors' deep knowledge of and respect for empirical biology. Even the most standard models are presented with nuanced observations on their strengths and limitations in capturing biological reality. This sets the book apart from many other recent works in evolutionary game theory, which are guided more by a love of mathematical beauty than by a true interest in biology. The treatment of matrix games – in which each player has only finitely many strategies – provides a case in point. These games have produced a rich and interesting mathematical theory, which is covered in depth by many texts. In practice, however, most traits are more naturally modelled as lying on a continuum. Matrix games certainly feature in McNamara and Leimar's book – they are pedagogically useful, after all. The authors are quick to point out the limitations of such games, however, and they treat continuous traits with the respect they deserve.

The mathematical approach of this book largely stays true to Maynard Smith's original conception of evolutionary game theory. The main focus is on evolutionary equilibria, with much less emphasis on how or whether such states can be reached (although stability does receive a fairly thorough treatment). The authors briefly criticize replicator dynamics, arguing in contrast that adaptive dynamics stays "somewhat closer to the population-genetic underpinnings". However, even adaptive dynamics is mostly treated as a tool to locate and characterize stable states, rather than as interesting in its own right. I was a little disappointed by this omission, especially in the context of multiple coevolving traits, where adaptive dynamics can potentially tell us a lot about which equilibria are likely to be reached by evolution. Much of this information can't be gained from simpler arguments about equilibria and their stability. Another topic that I had hoped to read more about is the relationship between adaptive dynamics and two much older branches of evolutionary theory: population and quantitative genetics. The existing literature on these connections is scattered and highly technical, seemingly a perfect target for the authors' clear-headed prose. Perhaps they will grace us with their insights another time.

Despite the somewhat traditional mathematics, this book has much to offer the practising theoretician. I was particularly pleased by the thorough development of the concept of fitness proxies. This work puts much of current theoretical practice on a firmer footing, while illuminating some limitations of common modellers' shortcuts. McNamara and Leimar also spend much effort arguing for a 'larger' game theory that includes aspects of an organism's development and life history. Their most interesting material here concerns the evolution of learning. The authors argue convincingly that so-called 'small world' models, in which organisms evolve fine-tuned responses to every possible situation they might encounter, are inadequate for understanding animal behaviour. 'Large world' models instead specify the rules for learning in potentially very complex environments. It is these rules, rather than specific actions, that are fine-tuned by evolution. This area seems ripe for development, especially given the recent explosion of machine learning algorithms that have barely made inroads into evolutionary biology.

https://doi.org/10.1016/j.baae.2021.04.007
1439-1791/

Another focus of the book is on 'consistent' games, in which pay-off structures emerge organically by modelling an organism's entire life cycle, rather than being specified *a priori*. While I am fully convinced by the need for consistency in evolutionary models, my main impression of this material was 'too little, too late'. Many of the 'standard' models early in the book suffer from consistency problems, as the authors readily acknowledge. Often the gravity of these problems seemed to be swept under the carpet, however. One example: the evolution of biparental care between individuals differing in quality. The authors argue that high-quality individuals might evolve to invest more in offspring than do low-quality individuals. If greater investment induces larger costs, however, then high-quality individuals might perversely end up with lower overall fitness than their low-quality partners. However, this argument rests on an old-school cost/benefit model, where the future reproductive success of each party is treated as a fixed constant. In a fully consistent model, individuals of any quality would potentially breed many times, and breeding pairs would include all possible combinations of quality (e.g. high-high, high-low and low-low). It is not clear to me that the simpler model's predictions would hold up in this more realistic context.

Several features of this book make it ideally suited for graduate-level seminars and courses. The chapters are well-balanced, even in length, and build upon each other in a satisfyingly natural way. The exercises are pedagogically well designed, consisting of a mixture of plug-and-play calculations and simple proofs (the latter of which could be safely ignored by less mathematically confident readers). Commendably, the book also contains comprehensive solutions to the exercises as an appendix. Sadly absent, however, is any kind of computer code. This is a real pity, as code is an essential tool for exploring, solving and truly understanding many of the models presented. For instance, evolutionarily stable strategies can often only be found using numerical procedures, but this book provides only the vaguest idea of how to implement these. The handful of simulation models presented in this book are little more than sketches without the accompanying code. The 'companion website' would be the ideal home for such code, but, at least at the time of writing, it provides a poor companion to this excellent book.

Any criticisms above could rightly be characterized as 'complaining at a high level' (to borrow a German phrase: *Jammern auf hohem Niveau*). This is an excellent book by two extremely eminent theoreticians and it deserves a place on any ethologist's shelf (or laptop: it's also available as an eBook). The subtitle *Concepts and Frontiers* captures it well: this is a book that simultaneously refines our fundamental tools and looks forward to where evolutionary game theory might be ten years from now. Both budding theoreticians looking for a doctoral project and veterans writing their next grant proposal could do much worse than to read this book cover-to-cover.

Declaration of Competing Interest

None.

References

Kokko, Hanna (2007). *Modelling for Field Biologists and Other Interesting People*. Cambridge University Press.

Broom, Mark, & Rychtář, Jan (2013). *Game-Theoretical Models in Biology*. Chapman & Hall/CRC.

Jonathan M. Henshaw
Institute of Biology I (Zoology), University of Freiburg, Hauptstraβe 1, 79104 Freiburg, Germany
E-mail address: jonathan.henshaw@biologie.uni-freiburg.de