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Game models for living systems

Theoretical physics is part of mainstream physics, and has been for several centuries. All physics undergraduates are exposed to both theoretical and experimental physics, woven together as the warp and woof of the subject.

Theoretical biology is a younger subject, as is biology more generally. The role of theory, particularly theory expressed in explicitly mathematical terms (as it often must be), is less universally accepted. This shows at every level.

At the undergraduate level, no one would think of bowdlerising an introductory physics course by introducing Newton's laws of motion in purely verbal form, unbacked by their expression as differential equations. But in introductory biology courses, proof of the Hardy-Weinberg law (in the absence of selection, mutation, gene flow and drift, gene frequencies remain unchanged from generation to generation with random mating) is often seen as unacceptably complicated and "mathematical". Yet this simple demonstration that genetic variability is thus preserved answers a key problem that plagued Charles Darwin and that the a-mathematical biology of his day could not resolve.

At the research frontier, the situation varies among sub-disciplines of biology. In ecology, after rich seed-sowing in the early years of this century, and an often troubled flowering in the 1960s-70s, mathematically expressed theory is today widely seen as part of the fabric of the subject. By contrast, many laboratory-based immunologists are still sceptical about the relevance of mathematical models to understanding the workings of the immune system. They remain unimpressed, for example, by the fact that despite a decade and more of brilliant work illuminating how individual HIV viruses interact with individual immune system cells, we are still miles away from understanding why there is so long and variable an interval between infection with HIV and the onset of Aids. I believe such understanding will necessarily involve studying how large populations of viruses interact with large populations of immune system cells; here mathematical models, based on and tested against data, must play a part.

Evolutionary Games and Population Dynamics

By Josef Hofbauer and Karl Sigmund

Cambridge University Press, 323pp
£50.00 and £16.95
ISBN 0 521 62365 0 and 62570 X

This brings me to Josef Hofbauer and Karl Sigmund's book. Their earlier work, *Theory of Evolution and Dynamical Systems*, did an excellent job of bringing together the relevant mathematical theory and the underlying biological motivation in the general areas of ecology and evolution. They believe, however, that several developments over the past ten years have set the scene for a rather different book. Undergraduate and postgraduate courses in mathematical biology are increasingly common, while new mathematical ideas and applications have appeared. And in some ways most important, the authors say, "within the social sciences, game theory has gained a lot of ground; and within game theory, evolutionary and dynamical aspects have exploded".

The result is a book that is significantly more mathematically oriented than their earlier one. For example, the previous book took more than 100 pages to introduce the "replicator equation" (of which more below); in the present volume it strides onto the stage expecting instant recognition. There is much less in the way of biological motivation for the mathematics, and fewer illustrative applications. The justification is that Sigmund's *Games of Life* elsewhere covers the "ecology, genetics and sociobiology which introduced the biological ideas underlying the mathematical models", in more readable form and for a general audience.

Against this background, my comments on the present book are twofold. First, as a mathematical text on an important set of topics in theoretical biology, the book is superb. It is well organised and beautifully written. In choosing from the rich menu of mathematical topics broadly relevant to ecology, behaviour, evolution and even theoretical immunology, it shows good taste.

The book begins with two introductions, one for game theorists and one for biologists. But it quickly becomes clear that the mathematical demands will be, as the mathematicians say, non-trivial. After a first section on dynamical systems, which emphasises non-linear problems and chaos, the second section introduces the replicator equation. In broad terms, this equation describes how the rates of change of particular types (genotypes, strategies) in a population depend on their relative abundance and on their relative reproductive ability. This leads us into the wonderful, and often counter-intuitive world of the dynamics of games.

The third main section focuses on various approaches to understanding persistence or permanence in replicator networks and other dynamical systems. Finally, the fourth section is a somewhat more familiar survey of population genetics, albeit from the perspective of game dynamics.

My second main comment is that, despite this book's excellence within the idiom its authors chose, I like the earlier book better. This book projects a loving enthusiasm for elegant theorems and, by implication, a lesser regard for messy application, which does not soothe the doubts that some experimental biologists have about this sort of thing.

To return to the physics analogy, a subtle but important distinction is often made between theoretical physics and mathematical physics. The former deals, as it were, with Schrödinger's equation and quantum mechanics and stuff every physicist must know. The latter deals with Hilbert spaces and other more formal topics, which not every physicist need know. Insofar as the distinction between theoretical biology and mathematical biology exists — one symptom of theory's immaturity in biology is that this distinction rarely is aired — Hofbauer and Sigmund's book is mathematical biology.

By a series of coincidences that weave together many strands in this review, game theory can claim to have been born at the theoretically oriented Institute of Advanced Studies in Princeton by John von Neumann and Oskar Morgenstern. After 30 years of indecision, the IAS early this year appointed its first professor of biology. I am pleased that Martin Nowak, an ex-student of Sigmund's and a former Oxford colleague of mine, chose to give his enterprise the mainstream appellation of theoretical biology, and not mathematical biology.

Sir Robert May is chief scientific adviser to the UK government and head of its Office of Science and Technology. He has held chairs in theoretical physics and in zoology, but is really an applied mathematician.