preserved. Walcott himself was so insecure about academic acceptance of the reality of these forms that he sent specimens to famous contemporary collections around the world to prove that no fakery was involved. Such circumspect behaviour was typical of him.

In this biography, Ellis Yochelson plots Walcott's prior career in painstaking detail — a career that embraced administration as much as research, political lobbying as much as geological theorizing. Yochelson paints an interesting and minutely observed picture of geological science on the hoof in its heroic days. It may not seem so unusual to us Thatcherite survivors today, but Walcott was adept at selling the economic benefits of studies of Cambrian brachiopods, or Chinese trilobites, in ways that would leave our scientific bureaucrats dumbfounded. He lobbied senators and academics alike, progressing daily from gruelling committee hearings to suppers at exclusive Washington clubs, pursuing the cause of the Geological Survey by diplomacy and example.

Yochelson's account of the political shenanigans of the time is admirable — if a little wearing. Given Walcott's relentless daily shuffling among Washington's great and good, it occasionally tires the reader to be attached so closely to his coat tails. But such careful attention does illuminate the dedication of the true administrator. These days, we may be accustomed to think of the chief as the enemy of creativity, the arbiter who stifles imagination. No such distinction was apparent to Walcott, whose every administrative triumph seemed to be followed by a scientific coup.

Unfairly, perhaps, I longed for Yochelson to reveal Walcott's Achilles' heel. Was he a secret womanizer? Did he have an uncontrollable temper, perhaps? A weakness for rye? Apparently, he was a paragon of virtue in all departments. He won his intellectual battles by means of reason and astute alliances, he mastered complex political briefs, and in the interstices composed magisterial monographs; he loved his family loyally and deeply. His diary entries are mostly those of a cold fish — he never utters a hurrah even when awarded honorary doctorates or prestigious medals. The entries warm to a little more than tepid only when he records his grief over the loss of his first wife.

The real disappointment of Yochelson's life of Walcott is that it is only about 70 per cent of a biography. It stops suddenly at Walcott's appointment to the Smithsonian Institution. This is a pity — not least because we do not reach the later science, including the Burgess Shale. Maybe a second volume is promised? The scholarship is admirable, at least from the North American side. It is disappointing to find the 'British Walcott', Archibald Geikie, persistently misspelled, and the spelling of Welsh placenames is very approximate indeed. But Walcott's is a life that needed to be described, and Yochelson has more than done him justice. □

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Animal analysts who know their plays

Game Theory and Animal Behaviour
edited by Lee Alan Dugatkin and Hudson Kern Reeve
Oxford University Press: 1998. 320 pp. £55, $78.

Evolutionary Games and Population Dynamics
by Josef Hofbauer and Karl Sigmund
Cambridge University Press: 1998. 323 pp. £50, $69.95 (hbk); £16.95, $27.95 (pbk)

Marc Mangel

Mathematical models of all sorts have contributed deeply to our understanding of biology. These two volumes deal with game theory, which is the branch of optimization models (formalized by von Neuman and Morgenstern in 1944) in which the behaviour of an individual depends on the frequency of certain actions of other individuals in the population. Although it was originally envisioned as an economic theory, John Maynard Smith recognized in the early 1970s that formal game theory had much to offer to biology, particularly because some of the concepts that had only vague definition in economics, such as utility, had very clear definitions and implications in biology, such as fitness. The ideas of Maynard Smith, based on the notion of an evolutionarily stable strategy (roughly, a strategy that, when adopted by all the members of a population, prevents the invasion through natural selection of any alternative strategy), form the foundation of evolutionary game theory.

Mathematical applications in biology are as diverse as biology itself, ranging from knot theory through partial differential equations to optimization methods. Donald Ludwig once wrote, "the misleading term 'Mathematical Biology' suggests that some part of Biology is being taken over by Mathematics. Biological Mathematics would be a better term. Linear thinking and methods still dominate the applications of mathematics. Biological requirements deflect us from that easy path". Both books leave the easy path behind.

Dugatkin and Reeve's edited collection explores various mathematical methods and models in evolutionary game theory, including the Prisoner's Dilemma, the Hawk–Dove game, the Sequential Assessment game, and the War of Attrition Model. But it also describes many interesting examples of real-life animal behaviour, including games between foraging producers and scroungers, reciprocal grooming in impala, territorial defence by birds and spiders, animal communication, parent–offspring conflict, and colony founding by ants. There are many accounts of experimental tests of game theory models, along with clear discussions of the limitations of the game theory approach.

The quality of writing (often a problem in edited volumes) is uniformly good. The chapter by R. Gomulkiewicz is especially important, because it connects game theory, other optimization methods, and quantitative genetics with a focus on an empirical strategy for detecting adaptation and constraint. These different mathematical methods are often described in opposition to each other, when they should be viewed as different ways of seeing the same problem.

The starting point of Hofbauer and Sigmund's book is the replicator equation, which recognizes that the rate of change of a certain type in a population depends on its frequency and its expected reproduction, relative to the other types in the population. Many mathematical results from the past decade are included, so the book is up to date and could be used for a course in mathematical aspects of theoretical ecology. The book has two introductions: one for game theorists and one for biologists. Even so, most biologists will find it hard going. The first part could be used in an advanced course on population dynamics or ecological modelling; but even here there is some sophisticated mathematics and heavy-duty notation. For example, the fourth chapter begins with the Poincaré–Bendixson theorem and continues to Hopf's bifurcation theorem; these are elegant, important and beautiful theorems, but difficult.

In the middle two sections of the book, the authors provide an elegant tour of evolutionary game theory and its connections to the classical equations of population dynamics. They provide a few specific examples, such as the rock–scissors–paper game and the repeated Prisoner's Dilemma, which may help bring the mathematics into clearer focus.

The last part of the book connects dynamical systems and frequency dependent genetics, playing much the same role as the article by Gomulkiewicz in showing the connections between dynamical systems and genetics.

Reading these two books together is interesting because it focuses the difference between theoretical biology (Dugatkin and Reeve) and mathematical biology (Hofbauer and Sigmund) in much the same way that theoretical and mathematical physics differ. Together, they have something for anyone interested in game models in organismal biology. □

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