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## BOOKS

### THEORETICAL BIOLOGY: Viral Immunology from Math

A review by Charles R. M. Bangham and Becca Asquith\*

**Virus Dynamics** Mathematical Principles of Immunology and Virology  
Martin A. Nowak and Robert M. May  
Oxford University Press, Oxford, 2000. 249 pp. \$70, £40. ISBN  
0-19-850418-7. Paper, \$34.95, £19.50. ISBN 0-19-850417-9.

It is a widespread fallacy that what mathematics contributes to biology is quantification of an otherwise innumerate science. But experimental biologists have long been expert at measuring and quantifying. The real contribution of mathematics lies in a precise qualitative framework of reasoning. The rate-limiting step in the advance of biology is usually experiment, not theory. (One of the very few notable exceptions was the theory of evolution by natural selection.) Experiment, however, is in no sense superior to theory, nor vice versa: both are necessary ingredients of a proper understanding of nature. An experiment done with no theoretical framework to analyze or interpret the results (let alone a hypothesis) is meaningless; theory in the absence of experiment remains mere theory.

Mathematics now occupies a central position in ecology, evolution, and genetics, and it has provided vital contributions to countless other areas of biology such as nerve conduction. But until recently it made little impact on immunology, largely because of our ignorance of much of the basic biology. In the last decade, immunologists have realized that the dynamics of the response to an infection within one host might be amenable to mathematical analysis. Such analysis is particularly applicable to viral infections, because of the relatively simple genetic structure of viruses and the rapidity with which they reproduce and generate genetic variation. In addition, experiments using viral infections to test evolutionary hypotheses can often be completed in days; viruses provide the kinds of sample numbers and reproductive rates that epidemiologists and animal geneticists can only dream about.

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Martin Nowak and Robert May have played an important part in the development of this field. In *Viral Dynamics*, they offer "a personal view of one emerging and potentially highly useful area" of the subject rather than an exhaustive textbook on theoretical immunology. Both authors come to the subject from theory and mathematics, not from experiment. As a result, the biology is pared down to the minimum and sometimes reads like a student's lecture notes. This approach may annoy some experimental biologists, because it can give the impression that the authors long to escape from the overgrown jungle of experiment into the clear air of theory. But it carries the advantages of precise and economical reasoning, and it demonstrates the wealth of conclusions that can follow from a small number of assumptions.

The HIV epidemic has given the field a strong impetus and a natural focus, so it is no surprise to find that most of the book is concerned with the dynamics of HIV-1. The chief questions the authors tackle are the most important in HIV-1 biology: Why does the CD4+ T cell count slowly and inexorably decline in most HIV-1-infected people? What part does the immune response play in limiting the progression of the infection? What is the role, if any, played in disease progression by the virus's immune escape? What determines the rate of emergence of drug resistance in HIV-1? What is the best strategy for drug treatment of the infection?

Although other virus infections are mentioned, particularly hepatitis B virus infection, there remains a danger that conclusions from HIV-1 infection are assumed to be generally true for all viruses, whereas there are often good reasons to suppose the opposite.

The authors rely on simple ordinary differential equations and basic linear algebra, and much of their discussion can be followed by anyone with a first-year-undergraduate training in mathematics. Readers with less mathematical background might wish that some steps in the reasoning were explained more fully. However, Nowak and May have tried hard (and, by and large, successfully) to give simple verbal renditions of the assumptions and conclusions in each chapter.

The ideal reader of *Viral Dynamics* will be someone prepared to bridge the gulf between theory and experiment. The book is more suited to one from the mathematical side of the gulf, but experimentalists will gain greatly from being asked for more precision about their assumptions and their reasoning. As biological knowledge becomes ever more complex and detailed, so natural language becomes more inadequate for certain types of biological questions. Mathematics provides an efficient, precise, and rigorous alternative; as the authors note, "mathematics is no more, but no less, than a way of thinking clearly." It is unfortunate that the authors omitted a chapter explaining the mathematical techniques they use to those biologists who wish to cross the gulf but lack the necessary mathematical training.

In the book's preface, Nowak and May emphasize the extraordinary disparity between the richness and sophistication of biological knowledge and the fundamental nature of certain questions that biology remains ill-equipped to answer. Mathematics provides an extremely useful tool to help answer some of these questions, by making possible thought experiments in which the variables can be precisely controlled. We hope that both mathematical and experimental biologists will read this book and bring their two fields closer together; both will gain.



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