Biomathematics

Volume 19

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Mathematical Biology

With 292 Figures

Springer-Verlag
Berlin Heidelberg GmbH

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Cover picture: A model based on a system of reaction-diffusion equations has been suggested by the author of this book to explain how the coat markings on the leopard and other mammals are generated. In this book, he gives a whole range of animal patterning examples - from the stripes on the zebra to the eyespots on the wings of butterflies - to demonstrate the wide applicability of such models.

Mathematics Subject Classification (1980): 34C, 34D, 35B, 35K, 92A06, 92A08, 92A12, 92A15, 92A17, 92A90

ISBN 978-3-662-08541-7

Library of Congress Cataloging-in-Publication Data.
Murray, J. D. (James Dickson)
Mathematical biology / James D. Murray.
p. cm. - (Biomathematics; v. 19)
Bibliography: p. Includes index.
ISBN 978-3-662-08541-7 ISBN 978-3-662-08539-4 (eBook)
DOI 10.1007/978-3-662-08539-4
1. Biology - Mathematical models. I. Title. II. Series
QH323.5.M88 1989 574'.072'4–dc19 88-34184 CIP

Originally published by Springer-Verlag Berlin Heidelberg New York in 1989
Softcover reprint of the hardcover 1st edition 1989

Media conversion: EDV-Beratung Mattes, Heidelberg
2141/3140-543210 Printed on acid-free paper

Preface

Mathematics has always benefited from its involvement with developing sciences. Each successive interaction revitalises and enhances the field. Biomedical science is clearly the premier science of the foreseeable future. For the continuing health of their subject mathematicians must become involved with biology. With the example of how mathematics has benefited from and influenced physics, it is clear that if mathematicians do not become involved in the biosciences they will simply not be a part of what are likely to be the most important and exciting scientific discoveries of all time.

Mathematical biology is a fast growing, well recognised, albeit not clearly defined, subject and is, to my mind, the most exciting modern application of mathematics. The increasing use of mathematics in biology is inevitable as biology becomes more quantitative. The complexity of the biological sciences makes interdisciplinary involvement essential. For the mathematician, biology opens up new and exciting branches while for the biologist mathematical modelling offers another research tool commmensurate with a new powerful laboratory technique but *only* if used appropriately and its limitations recognised. However, the use of esoteric mathematics arrogantly applied to biological problems by mathematicians who know little about the real biology, together with unsubstantiated claims as to how important such theories are, does little to promote the interdisciplinary involvement which is so essential.

Mathematical biology research, to be useful and interesting, must be relevant *biologically.* The best models show how a process works and then predict what may follow. If these are not already obvious to the biologists *and* the predictions turn out to be right, then you will have the biologists' attention. Suggestions as to what the governing mechanims are, may evolve from this. *Genuine* interdisciplinary research and the use of models can produce exciting results, many of which are described in this book.

No previous knowledge of biology is assumed of the reader. With each topic discussed I give a brief description of the biological background sufficient to understand the models studied. Although stochastic models are important, to keep the book within reasonable bounds, I deal exclusively with deterministic models. The book provides a toolkit of modelling techniques with numerous examples drawn from population ecology, reaction kinetics, biological oscillators, developmental biology, evolution, epidemiology and other areas.

The emphasis throughout the book is on the practical application of mathematical models in helping to unravel the underlying mechanisms involved in the biological processes. The book also illustrates some of the pitfalls of indiscriminate, naive or uninformed use of models. I hope the reader will acquire a practical and realistic view of biological modelling and the mathematical techniques needed to get approximate quantitative solutions and will thereby realise the importance of relating the models and results to the real biological problems under study. If the use of a model stimulates experiments – even if the model is subsequently shown to be wrong – then it has been successful. Models can provide biological insight and be very useful in summarizing, interpreting and interpolating real data. I hope the reader will also learn that (certainly at this stage) there is usually no 'right' model: producing similar temporal or spatial patterns to those experimentally observed is only a first step and does not imply the model mechanism is the one which applies. Mathematical descriptions are *not* explanations. Mathematics can never provide the complete solution to a biological problem on its own. Modern biology is certainly not at the stage where it is appropriate for mathematicians to try to construct comprehensive theories. A close collaboration with biologists is needed for realism, stimulation and help in modifying the model mechanisms to reflect the biology more accurately.

Although this book is titled *mathematical biology* it is not, and could not be, a definitive all-encompassing text. The immense breadth of the field necessitates a restricted choice of topics. Some of the models have been deliberately kept simple for pedagogical purposes. The exclusion of a particular topic – population genetics for example – in no way reflects my view as to its importance. However, I hope the range of topics discussed will show how exciting intercollaborative research can be and how significant a role mathematics can play. The main purpose of the book is to present some of the basic and, to a large extent, generally accepted theoretical frameworks for a variety of biological models. The material presented does not purport to be the latest developments in the various fields, many of which are constantly developing. The already lengthy list of references is by no means exhaustive and I apologise for the exclusion of many that should be included in a definitive list.

With the specimen models discussed and the philosophy which pervades the book the reader should be in a position to tackle the modelling of genuinely practical problems with realism. From a *mathematical* point of view, the art of good modelling relies on: (i) a sound understanding and appreciation of the biological problem; (ii) a realistic mathematical representation of the important biological phenomena; (iii) finding useful solutions, preferably quantitative; and what is crucially important (iv) a biological interpretation of the mathematical results in terms of insights and predictions. The mathematics is dictated by the biology and not vice-versa. Sometimes the mathematics can be very simple. Useful mathematical biology research is not judged by mathematical standards but by different and no less demanding ones.

The book is suitable for physical science courses at various levels. The level of mathematics needed in collaborative biomedical research varies from the very simple to the sophisticated. Selected chapters have been used for applied mathematics courses in the University of Oxford at the final year undergraduate and first year graduate levels. In the U.S.A. the material has also been used for courses for students from the second year undergraduate level through graduate level. It is also accessible to the more theoretically orientated bioscientists who have some knowledge of calculus and differential equations.

I would like to express my gratitude to the many colleagues around the world who have, over the past few years, commented on various chapters of the manuscript, made valuable suggestions and kindly provided me with photographs. I would particularly like to thank Drs. Philip Maini, David Lane and Diana Woodward and my present graduate students who read various drafts with such care, specifically Daniel Bentil, Meghan Burke, David Crawford, Michael Jenkins, Mark Lewis, Gwen Littlewort, Mary Myerscough, Katherine Rogers and Louisa Shaw.

Oxford, January 1989 *J. D. Murray*

If the Lord Almighty had consulted me before embarking on creation I should have recommended something simpler

Alphonso X (Alphonso the Wise), 1221–1284
King of Castile and Leon (attributed)

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* Denotes sections in which the mathematics is at a higher level. These sections can be omitted without loss of continuity.