

Nicholas F. Britton

Essential Mathematical Biology



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NICHOLAS F. BRITTON

Essential Mathematical Biology

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Aptech Systems, Inc., Publishers of the GAUSS Mathematical and Statistical System, 23804 S.E. Kent-Kangley Road, Maple Valley, WA 98038,
USA. Tel: (206) 432-7855 Fax (206) 432-7832 email: info@aptech.com URL: www.aptech.com

American Statistical Association: Chance Vol 8 No 1, 1995 article by KS and KW Heiner 'Tree Rings of the Northern Shawangunks' page 32 fig 2
Springer-Verlag: *Mathematica in Education and Research* Vol 4 Issue 3 1995 article by Roman E Maeder, Beatrice Amrhein and Oliver Gloor
'Illustrated Mathematics: Visualization of Mathematical Objects' page 9 fig 11, originally published as a CD ROM 'Illustrated Mathematics' by
TELOS: ISBN 0-387-14222-3, German edition by Birkhauser: ISBN 3-7643-5100-4.

Mathematica in Education and Research Vol 4 Issue 3 1995 article by Richard J Gaylord and Kazume Nishidate 'Traffic Engineering with Cellular
Automata' page 35 fig 2. *Mathematica in Education and Research* Vol 5 Issue 2 1996 article by Michael Trott 'The Implicitization of a Trefoil
Knot' page 14.

Mathematica in Education and Research Vol 5 Issue 2 1996 article by Lee de Cola 'Coins, Trees, Bars and Bells: Simulation of the Binomial Process'
page 19 fig 3. *Mathematica in Education and Research* Vol 5 Issue 2 1996 article by Richard Gaylord and Kazume Nishidate 'Contagious
Spreading' page 33 fig 1. *Mathematica in Education and Research* Vol 5 Issue 2 1996 article by Joe Buhler and Stan Wagon 'Secrets of the
Madelung Constant' page 50 fig 1.

British Library Cataloguing in Publication Data

Britton, N.F.

Essential mathematical biology (Springer undergraduate
mathematics series)

1. Biomathematics.

I. Title

570'.1'51

ISBN 185233536X

Library of Congress Cataloging-in-Publication Data

Britton, N.F.

Essential mathematical biology / N.F. Britton

p. cm. -- (Springer undergraduate mathematics series)

Includes index.

ISBN 1-85233-536-X (alk. paper)

1. Biomathematics. I. Title. II. Series.

QH323.5 .B745 2002

570'.1'51—dc21

2002036455

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Springer Undergraduate Mathematics Series ISSN 1615-2085

ISBN 1-85233-536-X Springer-Verlag London Berlin Heidelberg

a member of BertelsmannSpringer Science+Business Media GmbH

<http://www.springer.co.uk>

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Printed in the United States of America

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Typesetting: Camera-ready by author

12/3830-543210 Printed on acid-free paper SPIN 10844058

Preface

This book aims to cover the topics normally included in a first course on Mathematical Biology for mathematics or joint honours undergraduates in the UK, the USA and other countries. Such a course may be given in the second year of an undergraduate degree programme, but more often appears in the third year.

Mathematical Biology is not as hierarchical as many areas of Mathematics, and therefore there is some flexibility over what is included. As a result the book contains more than enough for two one-semester courses, e.g. one based on Chapters 1 to 4, mainly using difference equations and ordinary differential equations, and one based on Chapters 5 to 8, mainly using partial differential equations. However there are some classic areas that are covered in almost every course, the most obvious being population biology, often including epidemiology, and mathematical ecology of one or two species. Population genetics is also a classic area of application, although it does not appear in every first course. In spatially non-uniform systems there is even more choice, but reaction-diffusion equations are almost always included, with applications at the molecular and population level. Some large areas have been excluded through lack of space, such as bio-fluid dynamics and most of mathematical physiology, each of which could fill an undergraduate textbook on its own.

To cover the whole book the student will need a background in linear algebra, vector calculus, difference equations, and ordinary and partial differential equations, although a one-semester course without vector calculus and partial differential equations could easily be constructed. Methods only are required, and the necessary results are collected together in appendices. Some additional material appears on an associated website, at

<http://www.springer.co.uk/britton/>

This site includes more exercises, more detailed answers to the exercises in the book, and links to other useful sites. Some parts of it require more mathematical background than the book itself, including stochastic processes and continuum mechanics.

I would like to thank Jim Murray for his support and advice since my undergraduate days. I am grateful to all the (academic and non-academic) staff of the Department of Mathematical Sciences at the University of Bath for making this a genial place to work, the past and present members of the Centre for Mathematical Biology at the University of Bath for stimulating discussions, my students for their feedback on the lecture notes from which this book was developed, and Springer Verlag. Finally I would like to thank Suzy and Rachel for their love and support.

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1

Single Species Population Dynamics

- The first goal of this chapter is to understand how the rate of growth or decay of an isolated population is determined. This depends on modelling birth and death processes.
- Models of birth and death processes have a long history. Complicating factors are the dependence of birth and death rates on the age structure of the population, the effects of competition for resources, and delays in responding to environmental changes.
- We are interested in controlling as well as understanding population dynamics, and we shall discuss management strategies for fisheries.
- Spatial effects are increasingly being seen as important in fields such as conservation biology, and we shall introduce a simple method for investigating these.

1.1 Introduction

Attempts to understand population processes date back to the Middle Ages and earlier. Often, human populations were the focus of interest. Sir William Petty in about 1300 composed a table “shewing how the People might have doubled in the several ages of the World”, starting with 8 people one year after the Flood, 2700 years before the birth of Christ, and doubling at first every ten

years but then at successively longer intervals of time to arrive at 320 million (not a bad estimate) by the year 1300. Real data show that doubling times were about 1000 years over this period of time, but more importantly that they have become successively *shorter* to reach about 35 years in the later 20th century. The rate of population growth has therefore been faster than exponential, as we can see in Figure 1.1.

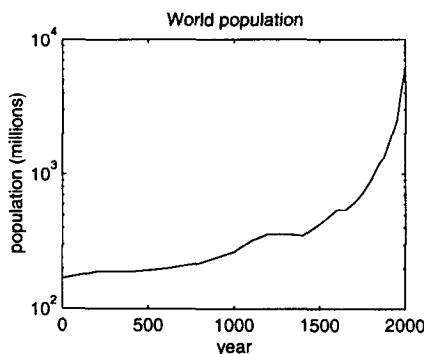


Figure 1.1 World human population growth over the last 2000 years. Exponential growth would give a straight line on this semilogarithmic plot.

Alternatively, we can think of this curve as exponential growth, but with an exponent that has (in general) increased over time. Population processes with parameters that change over time are called *non-stationary*; for simplicity, we shall restrict attention almost everywhere to *stationary* processes.

Human populations are exceptional in exhibiting exponential or faster growth over such a long time period. Most biological populations, except when colonising virgin territory, are regulated by competition for limiting resources or by other means. We shall look at population dynamics first in the absence of regulation, and then including regulatory effects.

1.2 Linear and Nonlinear First Order Discrete Time Models

Let us assume that the size N_n of a population at time n completely determines its size at time $n + 1$. The use of discrete time is sometimes rather artificial, but it may be appropriate if the population is censused at intervals, so that data for births and deaths are only available for discrete time periods. Such a model is sometimes called a *metered* model, especially when used in the fisheries context. Consider a continuously breeding population, such as a human population, censused at intervals. Let the probability of any given individual dying between

censuses (the *per capita mortality*) be d , and let the average number of births to any given individual in the same time period (the *per capita production or reproduction*) be b . Then the total number of deaths is dN_n , the total number of births bN_n , and so $N_{n+1} = (1 + b - d)N_n = \lambda N_n$, say. Alternatively, a discrete time model may be used for creatures that reproduce at a specific time of year, the breeding season, as we shall see in the next subsection.

The simplest first order model is therefore linear,

$$N_{n+1} = \lambda N_n, \quad (1.2.1)$$

known as the *Malthusian* equation in discrete time. The parameter λ is called the (*net*) *growth ratio*. If the process is stationary, λ constant, its solution with initial condition N_0 given is $N_n = N_0 \lambda^n$, which is geometrically growing with growth ratio λ if $\lambda > 1$. This is known as *Malthusian growth*. In 1798, Thomas Malthus published an Essay on the Principle of Population in which he stated that “population, when unchecked, increases in a geometric ratio”. He went on to say that subsistence increases in an arithmetic ratio, and to discuss the dire consequences of this difference. The phrase “when unchecked” is crucial, and Malthus recognised that such checks were constantly in place. However, the unchecked growth equation (1.2.1) and the equivalent equation in continuous time have come to bear his name.

1.2.1 The Biology of Insect Population Dynamics

Insects often have well-defined annual non-overlapping generations. For example, adults may lay eggs in spring or summer, and then die. The eggs hatch out into larvae, which eat and grow and then overwinter in a pupal stage. The adults emerge from the pupae the following spring. We have to decide at what time of year to take a census. Let us count adults at the breeding season, and let the average number of eggs laid by each adult be R_0 . The parameter R_0 is the *basic reproductive ratio*, defined to be the average number of offspring produced over a lifetime, all of these offspring in this case being produced at the same time. It is clear that this is a crucial parameter, and it will recur many times in this book. It is often used to represent not the total number of offspring produced, but the number that would survive to breed in the absence of the particular effect that is being studied. In an unchecked insect population with no premature mortality, Equation (1.2.1) therefore applies, with $\lambda = 1 + b - d$, $b = R_0$ and $d = 1$, so that the growth ratio λ is the basic reproductive ratio R_0 .

In a real insect population, some of the R_0 offspring produced by each adult will not survive to be counted as adults in the next census. Let us assume that

a fraction $S(N)$ do survive, this survival rate depending on N . The Malthusian equation is replaced by

$$N_{n+1} = R_0 S(N_n) N_n, \quad (1.2.2)$$

which may alternatively be written

$$N_{n+1} = N_n F(N_n) = f(N_n). \quad (1.2.3)$$

Here $F(N)$ is the *per capita production* and $f(N)$ the *production* of a population of size N . The model is called *density-dependent* if the per capita production F depends on N , which we assume to be the case. Density-dependent effects can also occur if the per capita fertility rather than the per capita survival depends on the density.

The model may be criticised for being deterministic, and for taking no account of predators, prey, or competing species, or of abiotic influences such as the weather. It assumes that population size is regulated by density-dependent factors. The question of whether density-dependent or density-independent factors are more important was a source of great controversy in the middle decades of the last century, although it is clear that if the population is regulated, density-dependent factors must have a role to play. However, the purpose of models of this form is to investigate whether simple assumptions on how the population is regulated are supported by the data.

1.2.2 A Model for Insect Population Dynamics with Competition

We shall test the hypothesis that insect populations are regulated by intraspecific (within-species) competition for some resource which is in short supply. Typical resources are food and space. We shall interpret R_0 as the number of adults each adult in one generation would produce in the subsequent generation in the absence of competition. For simplicity in the exposition we shall assume that competition affects survival rather than fertility, and discuss it in terms of the survival fraction S or the per capita production F . There are various idealised forms of intraspecific competition that can be considered, defined as follows.

- *No competition*: then $S(N) = 1$ for all N .
- *Contest competition*: here there is a finite number of units of resource (these could, for example, be a fixed number of safe refuges). Each individual which obtains one of these units of resource survives to breed, and produces