Mark Kot

# Elements of Mathematical Ecology

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# Elements of Mathematical Ecology

*Elements of Mathematical Ecology* provides an introduction to classical and modern mathematical models, methods, and issues in population ecology. The first part of the book is devoted to simple, unstructured population models that, for the sake of tractability, ignore much of the variability found in natural populations. Topics covered include density dependence, bifurcations, demographic stochasticity, time delays, population interactions (predation, competition, and mutualism), and the application of optimal control theory to the management of renewable resources. The second part of this book is devoted to structured population models, covering spatially structured population models (with a focus on reaction-diffusion models), age-structured models, and two-sex models. Suitable for upper level students and beginning researchers in ecology, mathematical biology and applied mathematics, the volume includes numerous line diagrams that clarify the mathematics, relevant problems throughout the text that aid understanding, and supplementary mathematical and historical material that enrich the main text.

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# Preface

Ecology is an old discipline. The discipline was christened in 1866 by Ernst Haeckel, a well-known German evolutionary biologist. Haeckel was a neologist – he loved to invent new scientific terms. His most famous gems are *phylogeny* and *oecologie*. *Oecologie* and *ecology* take their derivation from the Greek *oikos*, house or dwelling place. Ecology, as envisioned by Haeckel, is the study of the houses and the housekeeping functions of plants and animals. It is the scientific study of the interrelationships of organisms, with each other, and with their physical environment. The *idea* of ecology is even older (Worster, 1994). It is closely related to 18th century notions of the balance or economy of nature reflected, most clearly, in Linnaeus's 1749 essay *Oeconomia Naturae* (Stauffer, 1960).

Ecology is also a diverse discipline. After all, it has all of life to account for. In the old days, it was common to divide ecology into two subdisciplines: *autecology*, the ecology of individual organisms and of populations, and *synecology*, the study of plant and animal communities. Ecology is now divided into many subdisciplines (see Table 1).

Several subdisciplines use mathematics. For example, behavioral ecology makes extensive use of game theory and of other brands of optimization. It is impossible to cover all of these subdisciplines in one short book. Instead, I focus on population ecology and engage in occasional forays into community ecology and evolutionary ecology. This book could, and perhaps should, have been entitled *The Dynamics of Biological Populations*.

The material in this book has been used to teach a two-semester course. There is, therefore, a dichotomy in these notes. The first semester of the course is devoted to unstructured population models, models that, in effect, treat organisms as 'homogeneous green gunk'. Unstructured population models have the advantage, at first, of simplicity. As one adds extra bits

Table 1. *Branches of ecology*

| | |
|---|---|
| Synecology | Landscape ecology<br>Systems ecology<br>Community ecology |
| Autecology | Population ecology<br>Evolutionary ecology<br>Behavioral ecology<br>Physiological ecology<br>Chemical ecology |

of biology, these models become more realistic and more challenging. The topics in the first half of the book include density dependence, bifurcations, demographic stochasticity, time delays, population interactions (predation, competition, and mutualism), and the application of optimal control theory to the management of renewable resources.

Variety, and variability, are the spice of life. We frequently ascribe differences in the success of individuals to differences in age, space (spatial location), or sex. The second half of this book is devoted to structured population models that take these variables into account. I begin with spatially-structured population models and focus on reaction-diffusion models. There is also tremendous interest in metapopulation models, coupled lattice maps, integrodifference equations, and interacting particle systems (Turchin, 1998; Hanski, 1999). However, my colleagues and I tend to leave this material for our advanced course. I follow with an overview of age-structured population models in which I compare integral equations, discrete renewal equations, matrix population models, and partial differential equations. I conclude with a brief introduction to two-sex models.

The emphasis in these notes is on strategic, not tactical, models (Pielou, 1981). I am interested in simple mechanistic models that generate interesting hypotheses or explanations rather than in detailed and complex models that provide detailed forecasts. You will also find many equations, but few formal theorems and proofs. Applied scientists and pure mathematicians both have reason to be offended! Because of the interdisciplinary nature of my class and because of my own preference for solving problems over proving theorems, I have tried to hold to a middle course that should appear natural to applied mathematicians and to theoretical biologists. I hope that this middle course will appeal to a broad range of (present and future) scientists. Failing that, I hope that you, gentle reader, can use this book as a springboard for more detailed applied and theoretic investigations.

# Acknowledgments

I have been blessed with excellent teachers and students. I wish to thank all my teachers, but especially William K. Smith, W. Tyler Estler, Richard H. Rand, Simon A. Levin, William M. Schaffer, Paul Fife, Jim Cushing, Stephen B. Russell, and Hanno Rund.

Stéphane Rey coauthored Chapter 9. Other former students, Michael G. Neubert, Emily D. Silverman, and Eric T. Funasaki, will recognize work that we published together. Michael Neubert used this material in a class and provided a number of useful comments and criticisms.

Several cohorts of students studied this material as Mathematics or Ecology 581 and 582 at the University of Tennessee or as Applied Mathematics 521 at the University of Washington. I thank these students for their enthusiasm and hard work. I am grateful to the University of Tennessee and the University of Washington and to my colleagues at these institutions for the chance to teach these courses.

The early drafts of this book could not have been written without several valuable pieces of software. I thank Joseph Osanna for troff, Brian W. Kernighan and Lorinda L. Cherry for eqn, Jon L. Bentley and Brian W. Kernighan for grap, Michael Lesk for ms, tbl, and refer, James J. Clark for groff, Bruce R. Musicus for numeqn, Nicholas B. Tufillaro for ode, and Ralph E. Griswold, Madge T. Griswold, and the Icon Project for the Icon programming language.

It has been a pleasure working with Cambridge University Press. I wish to thank Alan Crowden, Maria Murphy, Jayne Aldhouse, Zoe Naylor, and especially Sandi Irvine for all their efforts.

Finally, I want to thank my parents for their encouragement and interest and my wife, Celeste, for her encouragement, support, and desire to purchase the movie rights.

*Knoxville, Tennessee* Mark Kot

# Contents

# **Part I** Unstructured population models

# Section A
# SINGLE-SPECIES MODELS

## 1 Exponential, logistic, and Gompertz growth

Tradition dictates that we begin with a simple homogeneous population. This population is that 'homogeneous green gunk' that I referred to in the preface. I will represent the number (or sometimes the density) of individuals in this population by $N(t)$. I will also make frequent reference to the rate of change, $dN/dt$, and to the per capita rate of change, $(1/N)\,dN/dt$, of this population.

Let us assume that all changes in this population result from births and deaths and that the per capita birth rate $b$ and per capita death rate $d$ are constant:

$$\frac{1}{N}\frac{dN}{dt} = b - d. \tag{1.1}$$

The difference between the per capita birth and death rates, $r \equiv b - d$, plays a particularly important role and is known as the *intrinsic rate of growth*. Equation (1.1) is commonly rewritten, in terms of $r$, as

$$\frac{dN}{dt} = r\,N. \tag{1.2}$$

One must also add an initial condition, such as

$$N(0) = N_0, \tag{1.3}$$

that specifies the number of individuals at the start of the process.

Equation (1.2) is a linear, first-order differential equation. It is easily integrated, either as a separable equation or with an integrating factor, and it possesses the solution

$$N(t) = N_0\,e^{rt}. \tag{1.4}$$

This solution grows exponentially for positive intrinsic rates of growth and

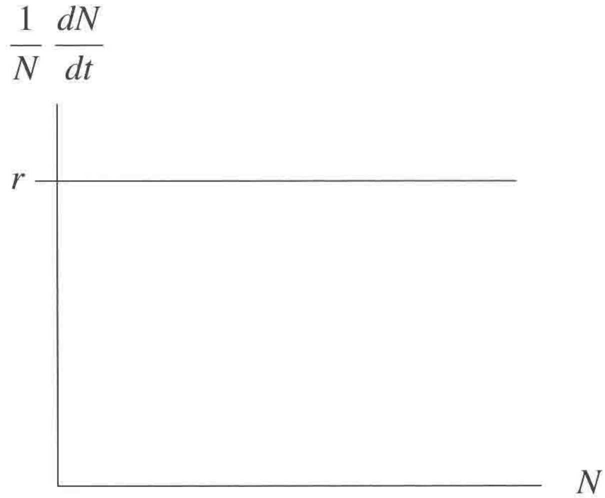


Fig. 1.1. Per capita growth rate.

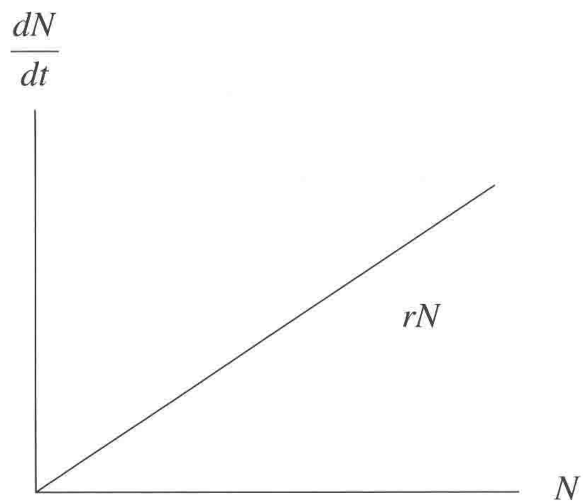


Fig. 1.2. Population growth rate.

decays exponentially for negative intrinsic rates of growth. It remains constant when births balance deaths.

Three different graphs capture the behavior of this system. In Figure 1.1, I have plotted the per capita growth rate as a function of the population size. The per capita growth rate remains constant for all population sizes: crowding has no effect on individuals. However, the growth rate for the entire population (Figure 1.2) increases with number as each new individual adds its own undiminished contribution to the total growth rate. The result (Figure 1.3) is a population that grows at ever-increasing rates.

The population size $N^* = 0$ is an *equilibrium point*. Since there is no

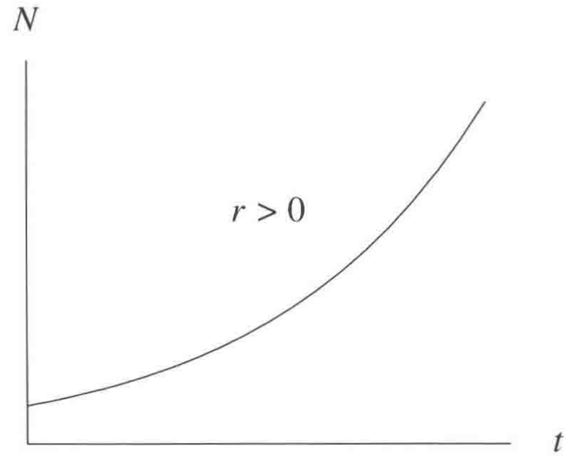


Fig. 1.3. Population trajectory.

immigration or emigration in this model, populations that start at zero stay at zero. For positive $r$, this equilibrium is *unstable*. After small perturbations, the population moves away from zero. For negative $r$, this equilibrium is *asymptotically stable*. Small perturbations now decay back to zero. I will say more about equilibria and stability later.

---

**Problem 1.1** ***Monod's† nightmare***

*Escherichia coli* is a bacterium that has been used extensively in microbiological studies. *Escherichia coli* cells are rod shaped; they are 0.75 $\mu$m wide and 2 $\mu$m long. Under ideal conditions, a population of *E. coli* doubles in just over 20 minutes.

(1) What is $r$ for *E. coli?*

(2) If $N_0 = 1$, how long would it take for an exponentially growing population of *E. coli* experiencing ideal conditions to fill your classroom?

---

There are several defects with this simple exponential model:

(1) The model has constant per capita birth and death rates and generates limitless growth. This is patently unrealistic.

(2) The model is deterministic; we have ignored chance or stochastic effects. Stochastic effects are particularly important at small population sizes.

† Jacques Monod (1910–1976) was the recipient of a 1965 Nobel Prize for Medicine for his work on gene regulation. He also conducted innovative experimental studies on the kinetics and stoichiometry of microbial growth (Panikov, 1995).

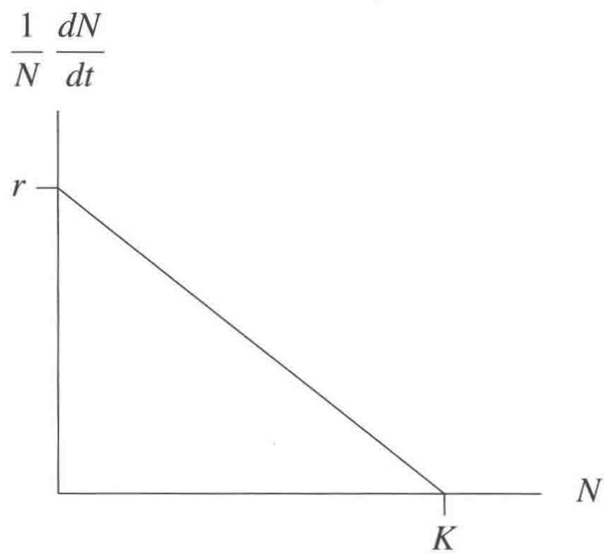


Fig. 1.4. Decreasing per capita growth rate.

(3) The model ignores lags. The growth rate does not depend on the past. Moreover, the population responds *instantaneously* to changes in the current population size.

(4) We have ignored temporal and spatial variability.

Let us start with the first defect.

What are the factors that regulate the growth of populations? There have been two schools of thought. In 1933, A. J. Nicholson, an Australian entomologist, published a seminal paper in which he stressed the importance of density-dependent population regulation. Nicholson (1933), the British ornithologist David Lack (1954), and others argued that populations are regulated by biotic factors such as competition and disease that have a disproportionately large effect on high-density populations. The opposing view, promulgated by the Australian entomologists H. G. Andrewartha and L. C. Birch (1954), is that populations are kept in check by abiotic, density-independent factors, such as vagaries in the weather, that have as adverse an effect on low-density populations as they do on high-density populations.

The dispute between these two schools occupied ecology for most of the 1950s (Tamarin, 1978; Kingsland, 1985; Sinclair, 1989). Density-dependent and density-independent factors may both be important in regulating populations. From a modeling perspective, however, it is easier to start with density-dependent regulation.

Consider a per capita growth rate that decreases linearly with population

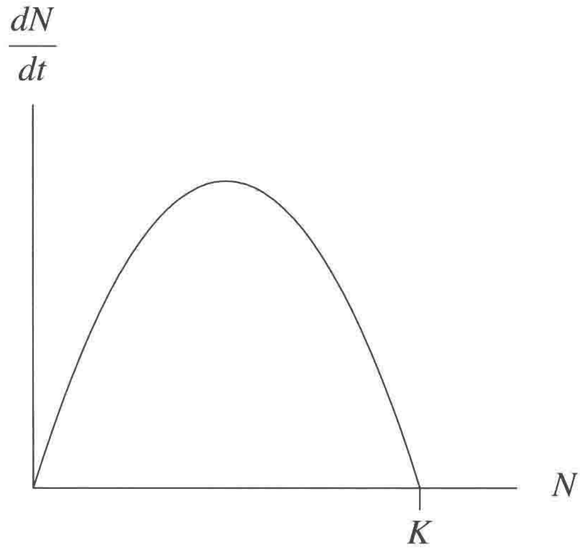


Fig. 1.5. Parabolic population growth rate.

size,

$$\frac{1}{N}\frac{dN}{dt} = r\left(1 - \frac{N}{K}\right) \tag{1.5}$$

(see Figure 1.4). This decrease in the per capita growth rate may be thought of as an extremely simple form of density-dependent regulation. Note that the per capita growth rate falls to zero at the *carrying capacity* $K$.

The population's growth rate,

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right), \tag{1.6}$$

is now a quadratic function of population size (see Figure 1.5). Equation (1.6) is known as the *logistic equation* or, more rarely, as the *Pearl–Verhulst equation.* It has an exact analytical solution. Figure 1.6 illustrates this solution for two different initial conditions. You are asked to find this closed-form solution in Problem 1.2. Since few nonlinear differential equations can be solved so easily, I will concentrate on a general method of analysis that emphasizes the qualitative features of the solution.

Equation (1.6) has two equilibria, $N^* = 0$ and $N^* = K$; at each of these two values, the growth rate for the population is equal to zero. Near $N^* = 0$, $N^2/K$ is small compared to $N$ so that

$$\frac{dN}{dt} \approx rN. \tag{1.7}$$

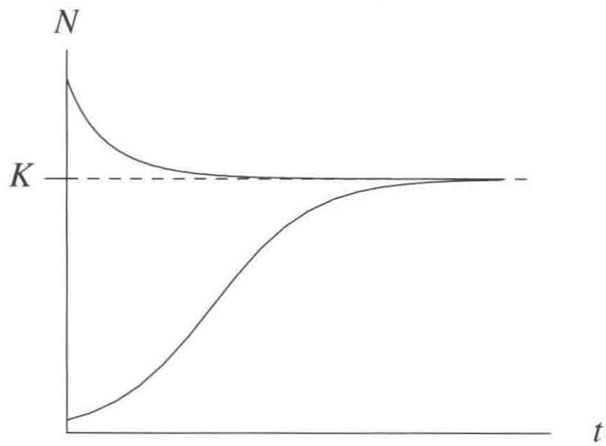


Fig. 1.6. Logistic growth.

For $r > 0$, small perturbations about $N^* = 0$ grow exponentially; the equilibrium $N^* = 0$ is unstable.

---

**Problem 1.2** ***Exact solution of the logistic equation***
Show that the logistic equation has the solution

$$N(t) = \frac{K}{1 + \left(\frac{K}{N_0} - 1\right) e^{-rt}} \tag{1.8}$$

(1) treating the logistic equation as a separable equation, and
(2) treating the logistic equation as a Bernoulli equation.

---

Close to $N^* = K$, we instead introduce a new variable that measures the deviation of $N$ from $K$:

$$x \equiv N - K. \tag{1.9}$$

Substituting $N = K + x$ into equation (1.6) gives us

$$\frac{dx}{dt} = -r\,x - \frac{r}{K}\,x^2, \tag{1.10}$$

and since $x$ is small for $N$ close to $K$, we have that

$$\frac{dx}{dt} \approx -r\,x. \tag{1.11}$$

For $r > 0$, small perturbations about $N^* = K$ *decay* exponentially; the equilibrium $N^* = K$ is asymptotically stable. For positive $r$, solutions to the