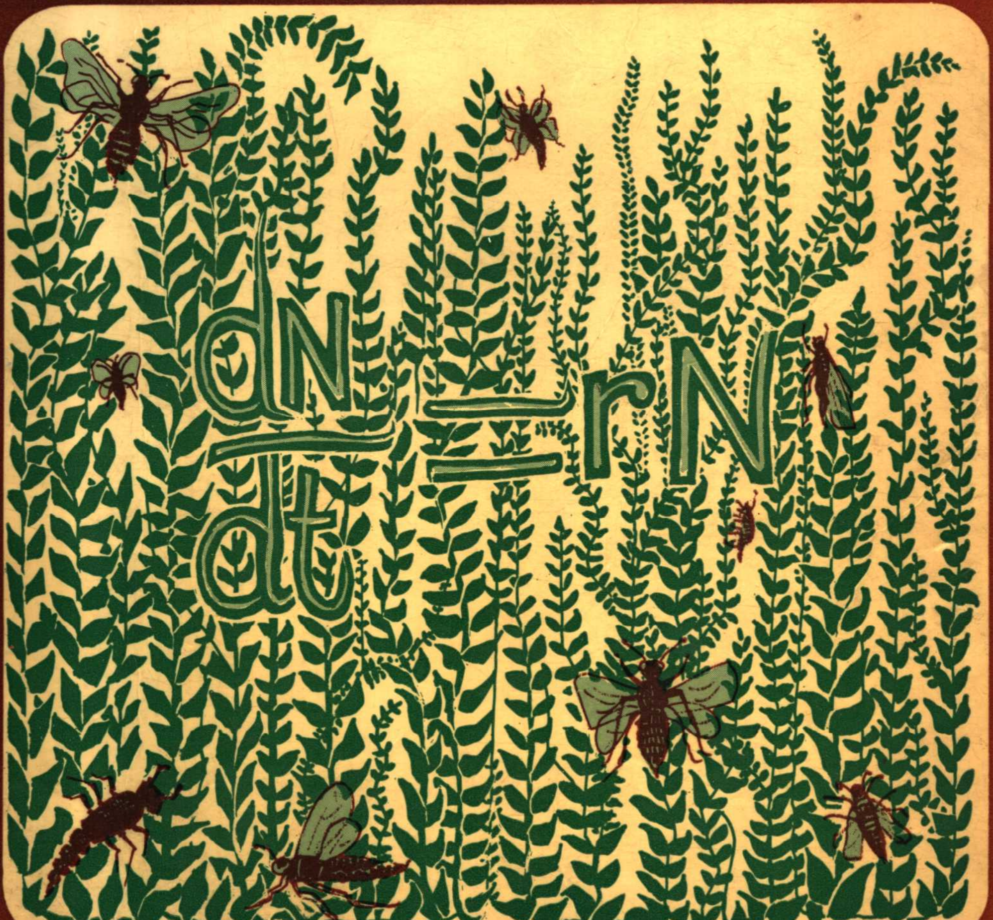
Theoretical Ecology

PRINCIPLES AND APPLICATIONS

Edited by Robert M. May



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In choosing the topics to be included in this book, I have exhibited a certain amount of bias and caprice; the guilt is entirely mine.

Princeton University R.M.M.
January 1976

Contents

1
Introduction

An increasing amount of study is being devoted to mathematical models which seek to capture some of the essential dynamical features of plant and animal populations. Some of these models describe specific systems in a very detailed way, and others deal with general questions in a relatively abstract fashion: all share the common purpose of helping to construct a broad theoretical framework within which to assemble an otherwise indigestible mass of field and laboratory observations.

The present book aims to review and to draw together some of these theoretical insights, to show how they can shed light on empirical observations, and to examine some of the practical implications. In so doing, the book seeks to occupy a useful niche intermediate between the compendious and general text (of which there are an increasing number of excellent examples) and the often highly technical journal and monograph literature on theoretical ecology (which many people will find impenetrable). The book is directed to an audience of upper level undergraduates, graduate students, or general readers with an educated interest in the discipline of ecology.

Attention is focussed on the biological assumptions which underlie the various models, and on the way the consequent mathematical behaviour of the models explains aspects of the dynamics of populations or of entire communities. That is, the approach is descriptive, with emphasis on the biological inputs in constructing the models, and on the emergent biological understanding. The intervening mathematical details are, by and large, glossed over; this is a book for people who did not get beyond a freshman course or A levels in calculus. Those readers who dislike ex cathedra pronouncements, or who wish to savour the detailed mathematical development, will find signposts to guide them to the more technical literature. Other people may be content to follow the advice given by St Thomas Aquinas (concerning technical details of proofs of the existence of God): 'Truths which can be proved can also be known by faith. The proofs are difficult, and can only be understood by the learned; but faith is necessary also to the young, and to those who, from practical preoccupations, have not the leisure to learn philosophy. For them, revelation suffices' (From Russell, 1946, p. 46).

As will be seen from the chapter headings, the first two-thirds of the book (chapters 2 to 10) deals with plant and animal ecology as such: theoretical and empirical aspects of the dynamics of single populations, of pairs of interacting populations, and of whole communities of different species. The last third of the book (chapters 11 to 14) is devoted to various subjects which are having fruitful reciprocal interaction with theoretical ecology. Although primarily aimed at review and synthesis, the book does contain a significant amount of new material.

Chapter 2 outlines the dynamical behaviour of single species in which population change takes place either in discrete steps, or continuously, subject to density dependent regulatory mechanisms with time-delays; the environment may be constant, or it may vary in time. The consequent population behaviour may be a stable equilibrium point (with disturbances damped in a monotonic or an oscillatory manner), or stable cycles, or even apparently random fluctuations, depending on the relations among the various natural time scales in the system. In chapter 2, these ideas are applied narrowly to the dynamical trajectories of particular laboratory and field populations, and in chapter 3 they are applied much more broadly to discuss the way an organism's bionomic strategy (size, longevity, fecundity, range and migration habit) is fashioned by its general environment.

Chapter 4 gives a brief survey of the basic dynamical features of two species interacting as prey-predator, as competitors, or as mutualists. This serves as a background to the next three chapters, which focus upon two special cases of the general prey-predator relationship, and upon competition. In chapter 5, mathematical models are combined with field and laboratory studies to elucidate the components of predation in arthropod systems. Chapter 6 does a similar thing for plant-herbivore systems. Competition is addressed in chapter 7, which shows how theory and empirical observation can illuminate such questions as the meaning of the ecological niche, or the limits to similarity among coexisting competitors.

Quantitative understanding of the populations' dynamics, of the sort which enlivens some of the earlier chapters, is rarely feasible for complex communities of interacting species. Here the search is more for broad patterns of community organization. Chapter 8 discusses some of these patterns: energy flow (where much progress has accrued from the work of the International Biological Program); relative abundances of the different species in the community; and convergence in the structure of geographically distinct communities in similar environments. Some of these notions can be developed further and applied to the biogeography of islands, and thence to the design and management of floral and faunal conservation areas; this is done in chapter 9. Chapter 10 presents a somewhat revisionist account of succession, arguing from theory and observation that ecosystems require occasional (neither too frequent, nor too infrequent) disturbance back to the zeroth successional state, if they are to maintain their potential diversity.

The final four chapters deal with areas on the edge of mainstream ecology. Chapter 11 summarizes some of the outstanding problems in sociobiology (the recently christened subject dealing with the structure and organization of animal societies). The way recent ecological advances may shed light on such long debated riddles as the great waves of extinction which mark the end of many of the conventional geological epochs is the subject of chapter 12, devoted to palaeobiology. Chapter 13 pursues the population biology of human host-parasite systems, such as schistosomiasis, while chapter 14 draws together ecology and economics in a discussion of optimal strategies for pest control.

I hope that the selection of topics has provided a representative range of examples where theoretical models have been successfully intermeshed with real world observations. More than this, I hope that the collection may convey a sense of excitement, and may, to some small degree, serve to indicate unanswered questions and future directions for research.

2
Models for Single Populations

ROBERT M. MAY

2.1 Introduction

One broad aim in constructing mathematical models for populations of plants and animals is to understand the way different kinds of biological and physical interactions affect the dynamics of the various species. In this enterprise, we are relatively uninterested in the algebraic details of any one particular formula, but are instead interested in questions of the form: which factors determine the numerical magnitude of the population; which parameters determine the time scale on which it will respond to natural or man-made disturbances; will the system track environmental variations, or will it average over them? Accordingly, attention is directed to the biological significance of the various quantities in the equations, rather than to the mathematical details; to do otherwise is to risk losing sight of the real wood in contemplation of the mathematical trees.

In this use of mathematical models to grasp at general principles, it is helpful to begin with models for a single species. Models of this kind seek to elucidate the behaviour of a single population, $N(t)$, as a function of time, t.

Many isolated laboratory populations, carefully maintained in a controlled environment, may realistically be modelled by such a single equation.

On the other hand, there are few, if any, truly single species situations in the natural world. Populations will tend to interact with their food supply (below them on the trophic ladder), with their competitors for these resources (on the same trophic level), and with their predators (above them on the ladder). In addition, populations will be influenced by various factors in their physical environment. Even so, it is often useful to regard these biological and physical interactions as passive parameters in an equation for the single population, summarizing them as some overall 'intrinsic growth rate', 'carrying capacity', or the like.

Section 2.2 discusses models where generations completely overlap and population growth is a continuous process (first order differential equations), and section 2.3 treats models where generations are non-overlapping and growth is a discrete process (first order difference equations). Some of the emergent insights are applied to field and laboratory data in section 2.4, and extended to encompass time-varying environments in section 2.5. Section 2.6 briefly discusses the more complicated case of many distinct but overlapping age classes. Section 2.7 concludes the chapter by reechoing the major themes.

2.2 Continuous growth (differential equations)

In situations where there is complete overlap between generations (as in human populations), the population changes in a continuous manner. Study of the dynamics of such systems thus involves differential equations, which relate the rate at which the population is changing, dN/dt, to the population value at any time, $N(t)$.

2.2.1 *Density independent growth*

The simplest such model has a constant per capita growth rate, r, which is independent of the population density:

$$dN/dt = rN. \tag{2.1}$$

This has the familiar solution

$$N(t) = N(0) \exp (rt). \tag{2.2}$$

There is unbounded exponential growth if $r > 0$, and exponential decrease if $r < 0$. In either event, the characteristic time scale for the 'compound interest' growth process is of the order of $1/r$.

2.2.2 *Density dependent growth*

Such unbounded growth is not to be found in nature. A simple model which captures the essential features of a finite environment is the logistic equation:

$$dN/dt = rN(1 - N/K). \tag{2.3}$$

Here the effective per capita growth rate has the density dependent form $r(1-N/K)$: this is positive if $N < K$, negative if $N > K$, and thus leads to a globally stable equilibrium population value at $N^* = K$. K may be thought of as the carrying capacity of the environment, as determined by food, space, predators, or other things; r is the 'intrinsic' growth rate, free from environmental constraints.

In any such dynamical system, it is useful to christen a 'characteristic return time', T_R, which gives an order-of-magnitude estimate of the time the population takes to return to equilibrium, following a disturbance (for a more formal discussion, see May *et al.*, 1974, and Beddington *et al.*, 1976a). In eq. (2.3), this characteristic time scale remains $T_R = 1/r$. To elaborate this point, we rewrite eq. (2.3) in dimensionless form by introducing the rescaled variables $N' = N/K$ and $t' = rt = t/T_R$. This gives the parameter-free equation

$$dN'/dt' = N'(1-N'). \tag{2.3a}$$

Such rescaling arguments are of general usefulness in disentangling those factors which influence the *magnitude* of equilibrium populations from those factors which bear upon the *stability* of the equilibrium. In this particular example, it is clear that the magnitude of the equilibrium population depends only on K, whereas the dynamics—the response to disturbance—depends only on r. This fact underlies the metaphor of r and K selection, developed in the next chapter.

It must be emphasised that the specific form of eq. (2.3) is not to be taken seriously. Rather it is representative of a wide class of population equations with regulatory mechanisms which biologists call density dependent, and mathematicians call nonlinear. A plethora of other such models, taken from the ecological literature, is catalogued in May (1975a, pp. 80–81). All share with eq. (2.3) the essential property of a stable equilibrium point, $N^* = K$, with any disturbance tending to fade away monotonically. One way of justifying eq. (2.3) is to regard it as the first term in the Taylor series expansion of these more general density dependent models.

2.2.3 *Time-delayed regulation*

In eq. (2.3), the density dependent regulatory mechanism, as represented by the factor $(1-N/K)$, operates instantaneously. In most real life situations, these regulatory effects are likely to operate with some built-in time lag, whose characteristic magnitude may be denoted by T. Such time lags may, for example, derive from vegetation recovery times or other environmental effects, or from the time of approximately one generation which elapses before the depression in birth rates at high densities shows up as a decrease in the adult population. A rough way of incorporating such time delays is to rewrite eq. (2.3) as

$$dN/dt = rN[1 - N(t-T)/K]. \tag{2.4}$$

This delay-differential equation was first introduced into ecology by Hutchinson (1948) and Wangersky and Cunningham (1957), and by now it enjoys an extensive literature (for a brief guided tour, see, e.g., May 1975a, pp. 95–98). One way of deriving it is as a crude approximation to a fully age-structured description of a single population, in which case T is the generation time. As before, the detailed form of this equation is not to be taken literally, and in more realistic treatments the regulatory term is likely to depend not on the population at a time exactly T earlier, but rather on some smooth average over past populations. (For a more mathematical discussion, see May, 1973a.) Nonetheless, the general properties of eq. (2.4) are representative of this wider class of models, and will be discussed in this spirit.

The qualitative nature of the solutions of eq. (2.4) follow from precepts familiar to engineers. If the time delay in the feedback mechanism (namely, T) is long compared to the natural response time of the system (namely, T_R or $1/r$), there will be a tendency to overshoot and to overcompensate. For modest values of the time delay this overcompensation produces an oscillatory, rather than a monotonic, return to the equilibrium point at $N^* = K$. As the time delay becomes longer (as T/T_R or rT exceeds some number of order unity), there is a so-called Hopf bifurcation, and the stable point gives way to stable limit cycles. These stable cycles are an explicitly nonlinear phenomenon, in which the population density, $N(t)$, oscillates up and down in a cycle whose amplitude and period is determined uniquely by the parameters in the equation. Just as in the case of a stable equilibrium point, if the system is perturbed it will tend to return to this stable cyclic trajectory. Such stable limit cycle solutions are a pervasive feature of nonlinear systems, for which conventional mathematics courses (with their focus on linear systems) give little intuitive appreciation.

Specifically, eq. (2.4) has a monotonically damped stable point if $0 < rT < e^{-1}$, and an oscillatorilly damped stable point if $e^{-1} < rT < \frac{1}{2}\pi$. For $rT > \frac{1}{2}\pi$, the population exhibits stable limit cycles, the period and amplitude of which are indicated in Table 2.1. These numerical details (e^{-1} and $\frac{1}{2}\pi$) are peculiar to eq. (2.4), but the character of the solution, with a stable equilibrium point giving way to stable cycles once T/T_R exceeds some number of order unity, is generic to a much wider class of models with time-delayed regulatory mechanisms.

Table 2.1. Properties of limit cycle solutions of eq. (2.4).

rT	N(max)/N(min)	Cycle period, T
1·57, or less	1·00	—
1·6	2·56	4·03
1·7	5·76	4·09
1·8	11·6	4·18
1·9	22·2	4·29
2·0	42·3	4·40
2·1	84·1	4·54
2·2	178	4·71
2·3	408	4·90
2·4	1,040	5·11
2·5	2,930	5·36

In particular, it is worth noting that once stable limit cycles arise in equations of the general form of eq. (2.4), their period is roughly equal to $4T$. A qualitative explanation of this fact is as follows: In the first phase of the cycle, the population continues to grow ($dN/dt > 0$) until the earlier population value in the time-delayed regulatory factor attains the potential equilibrium value ($N(t-T) = K$); at this point, population growth ceases ($dN/dt = 0$), and the population begins an accelerating decline from its peak value. Thus the first phase, where the population grows from around K to the cycle maximum, takes a time T. Similar arguments applied to the subsequent phases of the cycle suggest an overall period of roughly $4T$. The exact results in Table 2.1 show that this rough rule remains true, even as the amplitude of the cycle (population maximum/population minimum) increases over several orders of magnitude.

In short, equations such as (2.4) constitute minimally realistic models for a single population, in which the density dependent regulatory effects (derived from food supply limitations, or crowding, or whatever) operate with a time delay. The consequent population dynamics can be monotonic damping to an equilibrium point, or damped oscillations, or sustained patterns of stable cycles, depending on the ratio between T and T_R. A variety of population data can be surveyed in this light, and this is done in section 2.4 and in chapter 3.

2.3 Discrete growth (difference equations)

At the opposite extreme from section 2.2, many populations are effectively made up of a single generation, with no overlap between successive generations, so that population growth occurs in discrete steps. Examples are provided by many temperate zone arthropod species, with one short-lived adult generation each year. Periodical cicadas, with adults emerging once every 7 or 13 or 17 years, are an extreme example.

In these circumstances, the appropriate models are difference equations relating the population in generation $t+1$, N_{t+1}, to that in generation t, N_t. In contrast to section 2.2, time is now a discrete variable.

2.3.1 *Density independent growth*

The difference equation analogue of eq. (2.1) is the simple linear equation

$$N_{t+1} = \lambda N_t. \tag{2.5}$$

Here λ (conventionally misnamed the 'finite rate of increase') is the multiplicative growth factor per generation; the 'compound interest' growth rate is* $r = \ln \lambda$. Equation (2.5) describes unbounded exponential growth for $\lambda > 1$ ($r > 0$), exponential decline to extinction if $\lambda < 1$ ($r < 0$).

2.3.2 *Density dependent growth*

More generally, and more realistically, we will have a density dependent relation of the form

$$N_{t+1} = F(N_t), \tag{2.6}$$

where $F(N)$ is some nonlinear function of N. A fairly complete catalogue

* Throughout this volume, we follow the conventional practice of using ln to denote natural logarithms (to the base e), and log to denote logarithms to the base 10.