
Elementary Mathematical Ecology

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A Wiley-Interscience Publication

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FOR HARRY AND ELSIE

Preface

The inspiration for this volume came from teaching a course in mathematical ecology to a group of undergraduate and graduate biology students. I started putting together the notes from which this book evolved after four years of experience in teaching that course, during which I found that the math anxiety of the students was frequently a real handicap to their desire to understand mathematical ecology.

To sidestep this anxiety I developed a problem-solving approach to the subject, starting with extremely straightforward problems and progressing to the more complex as the students grew in understanding and self-confidence. Judging from both student claims and their actual performance on exams, this approach has been extremely effective. Students routinely report that for the first time in their lives a mathematical subject makes sense to them and that the progressive nature of the problems makes it such that the mathematics never seems to get any more difficult.

My original notes have been class-tested now for seven years and revised each year on the basis of the students' comments and criticism. This book now includes the ideas of more than 150 advanced undergraduate and graduate biology students. Particular care has been taken to ensure that when the text is actually worked through, not just skimmed, the difficulty of the problems progresses in easy stages. Thus, in Chapter 1 students encounter an extremely elementary introduction to the nature of the exponential function but by Chapter 8 are asked to compute eigenvalues for systems of differential equations.

The mathematics required for this text is basic calculus and elementary linear algebra. One need not, however, be brilliant in these two fields. A basic gut-level knowledge of calculus (understanding the concept of a derivative and integration and being able to integrate and differentiate simple functions) and a working knowledge of elementary matrix manipulations (matrix addition, subtraction, multiplication, and an intuitive understanding of the inverse of a matrix) are quite sufficient. Much of the necessary mathematics is explained in the text. After completing this book the student should have a working knowledge of the important mathematical techniques needed to appreciate the contemporary ecological literature. It is not, however, intended as a complete survey of the latest developments in theoretical ecology.

As in any book of this sort, the individuals who contributed in one way or another to its formation are too numerous to mention. Two people must be singled out for special thanks: Robert MacArthur who not only introduced me to most of the topics herein but was also the first to point out to me the problem of math anxiety faced by most biology students, and Steve Hubbell who originally taught the course with me and suggested the problem-solving approach.

Finally, a great deal of thanks must go to approximately 150 undergraduate and graduate students at the University of Michigan whose comments and criticisms forced me to revise the text seven times to reach its current level. The book is as much theirs as it is mine.

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Introduction

Gaining access to the literature in contemporary ecology has become a different task than it was 15 years ago. Today a background in mathematics is a requirement for the serious ecologist. Without a working knowledge of certain mathematical concepts the current ecological literature is virtually meaningless. Although the training of students in ecology usually includes a brief exposure to the more historically important mathematical results, it is only the exceptional student who will make a special effort to develop an understanding of the mathematical concepts that are at the base of the latest in the literature. Yet the ability to use that literature to the full rests on that understanding. The problem is that the average ecologist has a great deal of difficulty keeping up with modern trends. The material herein represents an attempt to fill the void and to provide students with an approach to many of the mathematical techniques that are needed to appreciate contemporary ecological knowledge. It is not intended as a complete, up-to-date exposition of the "latest" developments in theoretical ecology.

This book was designed as a "programmed" learning text. Consequently there is a specific way in which it should be used for maximum effectiveness. It does not contain the sort of material that one can read casually, regardless of how carefully one reads or the quality of one's background. The explanatory material is not meant to stand alone and therefore if one concentrates on it a confusing picture may emerge. Rather, the exercises must be worked out as they are presented. The following outline should be adhered to closely:

- 1 Read the explanatory material until you come to a set of exercises.
- 2 *Before reading any further* do the exercises.
- 3 Each exercise should be attempted without reference to the answer at the end of the chapter. If the way in which the exercise should be done is not evident after a few minutes of thought, look at the answer to determine general drift but not in great detail. Go back and try it again.
- 4 After all exercises in a section have been completed (and only then) go on to the next section of explanatory material and repeat the process.

As you complete the exercises be sure to check the answers at the end of the chapter to make sure you have done them as I did. It is not that there is only one way of doing them but that frequently the result of a particular exercise is used in subsequent exercises. If your answers do not correspond to mine, you may become confused in later exercises.

Frequently the motivation for an exercise is discussed after the exercise, perhaps a strange concept at first glance. I have found that it is most effective pedagogically to have had experience with the mechanics of solving a problem before the underlying principles are introduced. For some concepts the mechanics become confused with the principles if they are introduced simultaneously. Thus, when you approach a particular exercise and find that you really do not understand why you have been asked to do it in the first place, please have patience. Its rationale will be made evident either in subsequent exercises or in the explanatory text.

It is worth emphasizing that the two parts of this text (explanatory material and exercises) are intimately related. The text was *not* written to allow you to read the explanatory material and skip the exercises. The exercises are an integral part of the whole—indeed probably more important than the other material. Many concepts are introduced *only* in the exercises and often the explanatory material is intimately dependent on these concepts.

The exercises have been developed on the basis of seven years of classroom testing and both their number and the amount of repetition are carefully geared to giving the student enough experience with each problem to grasp it effectively. Some concepts are mastered only after enough practice has been gained in dealing with the mechanics of the computations involved in their application.

By and large I have tried to keep the chapters to the same “effective” length; that is, each chapter should require about the same amount of time for completion. Unfortunately, as judged by student use, I have not been entirely successful. Some of the chapters are harder than others conceptually; others require more repetitive calculations. On the whole you should find yourself spending three to seven hours on each chapter. If you find you need more time, you may not have the proper background for this textbook.

It may be apparent that the notation is not always consistent from chapter to chapter. This is not an oversight. When you go to the literature to study these techniques in recent work, you will find considerable variation in the notation from paper to paper. Indeed such a state seems to be one source of difficulty for students first trying to read the literature in theoretical ecology. For each type of problem I have tried to use the notation most commonly encountered in that topic.

1. The Exponential and Logistic Equations

THE EXPONENTIAL EQUATION. We begin our study of demography by stripping it of all of its complicated details. To make clear the underlying processes that can be objectively and rigorously quantified, we reduce the individuals in a population to particles that do nothing but replicate themselves. So, if we begin with one individual at the present time, we will have two individuals some time in the near future. For the sake of simplicity let us assume that all individuals in the population replicate (produce a baby) after a particular time unit (one day, 30 years, etc.). Suppose, in particular, that each individual replicates once each day (produces one new individual each day). Then, if at day zero we start with one individual, by day 1 we will have two, by day 2 we will have four, by day 3 we will have eight, and so on. If we call the number of individuals in the population at some particular time $N(t)$, we have, for the above example, $N(0) = 1$, $N(1) = 2$, $N(2) = 4$, $N(3) = 8$, and so on.

□ EXERCISES

- 1 If every individual produces one baby per day, how many individuals will be in the population after four days if $N(0) = 15$? If $N(0) = 35$? (Assume that no deaths occur and that a baby produced today does not reproduce until tomorrow.)
- 2 If every individual produces four babies per day and $N(0) = 5$, what will be the values of $N(1)$, $N(2)$, $N(3)$, $N(4)$? (Assume here, as in the preceding exercise, that no deaths occur and that a baby produced today does not reproduce until tomorrow).
- 3 Repeat exercise 2 for $N(0) = 10$.
- 4 Compute $N(t)$, $t = 5, 6, \dots, 10$, for the example in exercise 2 and plot $N(t)$ against t . □

Thus, if the series we generate $t = 0, 1, 2, 3, 4, \dots$, is $1, 2, 4, 8, 16, \dots$, obviously we can represent the relationship between $N(t)$ and t as

$$N(t) = 2^t \tag{1}$$

The number 2 may be written in numerous ways ($\frac{4}{2}$, 2×1 , 0.5^{-1}). In particular, it can be written $2 = a^r$, where there are infinite combinations of a and r which, when plugged into a^r , will yield the number 2; but we are concerned with one particular value of the constant a . The value that we allow a to assume, by convention, is Euler's constant: $e = 2.71828 \dots$. If you have recently had calculus, you probably know why it is convenient to let $a = e$. If you have forgotten your calculus, be sure that you understand that it is *valid* to represent 2 (or, for that matter, any other number) as e^r and that it would be equally valid to represent it in other ways, but that for reasons that are merely convenient and need not concern you we choose e^r , where e is Euler's constant and r is a constant. Specifically, if $e^r = 2$, $r = 0.693$ (recall that by definition $\ln e^r = r$; therefore, if $e^r = 2$, $\ln 2 = r$). Equation 1 then becomes

$$N(t) = e^{(0.693)t} \quad (2)$$

Note that in this exercise, as well as in the rest of this book and in all of the literature, $N(t)$ is variously written as $N(t)$ or N_t or sometimes $X(t)$ or X_t , depending on the author or context. Frequently the functional dependence on t is tacitly assumed; that is, $N(t)$ may be written as N and $N(0)$ is almost always written as N_0 .

□ EXERCISES

- 5 Present the model populations in exercises 2 and 3 in the general form of equation 2.
- 6 If an individual produces 0.5 offspring per day (on the average) and we begin with a population size of 2, what is $N(15)$?

Equation 2 was written explicitly with the assumption that we began with a single individual; that is, when $t = 0$, $N(t) = 1$. To be more general we must multiply the right-hand side of equation 2 by $N(0)$, the number of individuals we started with, to obtain

$$N(t) = N(0)e^{rt} \quad (3)$$

as the general equation of population growth. It is called the exponential equation. The parameter r is central to population ecology. Mathematically it is the parameter of the exponential equation (equation 3) and biologically it is called the intrinsic rate of natural increase. This concept is discussed at length in later chapters. For now you should have an intuitive feeling for what it means (i.e., the number to which Euler's constant must be raised to obtain the replication (reproductive) rate, as introduced in this chapter).

We note that we may rewrite equation 3 as

$$\ln N(t) = \ln N(0) + rt$$

and differentiate with respect to t :

$$\frac{d \ln N(t)}{dt} = r$$

Recall from basic calculus that in general

$$\frac{d \ln x}{dt} = \frac{d \ln x}{dx} \frac{dx}{dt} = \frac{1}{x} \frac{dx}{dt}$$

Therefore

$$\begin{aligned} \frac{d \ln N(t)}{dt} &= r \\ \frac{1}{N(t)} \frac{d N(t)}{dt} &= r \\ \frac{d N(t)}{dt} &= r N(t) \end{aligned} \tag{4}$$

Equation 4 is a differential equation and equation 3 is its integrated form. Both are termed the exponential equation of population growth or simply the exponential equation.

□ EXERCISES

- 7 If r is 0.69, what is the replication rate (number of offspring per day + 1; 1 represents the adult doing the reproducing)? What if $r = 1.098$? What if $r = 0.92$? What if $r = 1.39$? What if $r = 4.5$? What if $r = 6.8$?
- 8 Let $r = 0.83$ and begin with a population size of 2. Plot $N(t)$ against t for $t = 0, 1, \dots, 6$.
- 9 Plot $\ln N(t)$ against t for $t = 0, 1, 2, \dots, 6$, for the data in exercise 8. If you wanted to compute r from this graph, how would you do it?
- 10 What is the doubling time (how long will it take for the population to double in size) if $r = 0.993$ and $N(0) = 10$? If $r = 0.993$ and $N(0) = 20$?
- 11 Derive a general equation for doubling time; for tripling time. □

To this point we have examined in the abstract a self-replicating population of particles. Clearly, even at this oversimplified level we have glossed over some fairly universal and important biological facts. Most organisms don't "replicate" like DNA or carbon paper. Most organisms are born, live, and die and we must be concerned with the rate of birth and death, not with the rate of replication.

The usual procedure is to look at the per capita rate of population increase. The per capita rate of increase must be equal to the birth rate minus the death rate. Thus we may write

$$\frac{d N(t)}{N(t) dt} = b - d \quad (5)$$

and we then see from equation 4 that $b - d = r$.

Intuitively, nothing changes. Instead of visualizing a population with individuals replicating themselves at some rate, we conceive of them as producing offspring and being subjected to a certain probability of dying such that as a whole the population can be said to have a death rate.

□ EXERCISES

- 12 In a population of *Paramecium* it is known that under a well-defined set of circumstances each *Paramecium* will divide twice in one day (i.e., in one day a single *Paramecium* turns into four individuals. In terms of the preceding exercises you might think of each individual as producing three babies.) Death is unknown. What is the "instantaneous" birth rate (b in equation 5)? What is the intrinsic rate of increase?
- 13 Suppose that in the course of dividing (in the example from exercise 12) 50% of the time the individual that was to divide died instead. What are b , d , and r ?
- 14 Repeat exercise 13 but assume that 25% of the attempted divisions resulted in death.

DENSITY DEPENDENCE. The most trivial observations of the most casual observer will reveal a basic inadequacy in the exponential equation, at least insofar as it might be applied to real populations. The equation, if taken as a model that is supposed in some way to represent a natural population, leads to a blatant prediction. Populations grow without limit. It is not necessary to cite experimental evidence to show that the prediction is not borne out in nature.

Two schools of thought emerged from the realization that populations are somehow limited in their growth (i.e., cannot follow the exponential equation forever). One school, typified by the well-known book by Andrewartha and Birch (1954), claimed that most populations did, in fact, follow the exponential equation but that frequently, at more or less random intervals, the population is decimated by some catastrophic event. Thus natural populations behave in a stop-and-start fashion, growing exponentially until some "disaster" forces the population numbers down. The critical feature of this sort of approach is that the factor that knocks the population down is independent of the number of individuals in the population. The other school emphasized the feedback of population numbers on population growth rate. As the number of individuals in the population became larger there was a decrease in the rate at which new individuals were produced and/or an increase in the likelihood of individuals dying. Thus the basic form of population growth was not really exponential

because the rate of growth was a decreasing function of the size of the population. (For a summary of the debate see Erlich and Birch [1967] and Slobodkin, Smith, and Hairston [1967].)

Most biologists now agree that many, if not all, natural populations are, at least potentially, subject to these density-dependent constraints (even the strictest adherents to the density-independent school will admit that *some* populations are controlled by density-dependent factors). Thus it makes sense to modify the basic picture of population growth as presented above to account for population limitation of the density-dependent type.

In a general way we may say that the per capita rate of change is a function of population size; that is,

$$\frac{dN}{N dt} = f(N)$$

and simply note that $f(N)$ gets smaller as N gets larger (i.e., $\partial f / \partial N < 0$) and that f is largest as N approaches zero (i.e., any function that satisfies these two assumptions will provide us with a “reasonable” model of density-dependent population growth). Making a convenient mathematical assumption, we let f take on a simple linear form; that is, we suppose that when N is very small ($N \rightarrow 0$) the population grows like an exponential equation (in a density-independent fashion) and for every individual added to the population the per capita growth rate is decreased by a particular amount. Thus the differential equation of population growth becomes

$$\frac{dN}{N dt} = r - aN \quad (6)$$

where a is an arbitrary constant that represents the “particular” amount the growth rate is decreased by the addition of a single individual.

□ EXERCISES

- 15 For what values of N will the per capita rate be equal to zero (in equation 6)?
- 16 Call the largest value of N for which $dN/N dt = 0$ the carrying capacity (K) and rewrite equation 6 in terms of K , r , and N only.
- 17 Suppose that the maximum number of individuals sustainable by the environment is K . Suppose that the per capita rate of increase of the population is directly proportional to the fraction of K not yet attained. What would $f(N)$ be? □

The equation derived in exercises 16 and 17 is called the logistic equation and is usually written

$$\frac{dN}{dt} = rN \left(\frac{K - N}{K} \right) \quad (7)$$

Equations 6 and 7 are, of course, identical; the form presented in (7) is more common only because it has such obvious biological interpretations. The logistic equation is but one of an infinite number of equations that describe a process of density-dependent population growth. The logistic has the simple property that it describes a population which initially increases at an increasing rate (like an exponential), but as N gets larger the rate of increase becomes smaller until N reaches a maximum value (K), after which the population size no longer changes.

This derivation of the logistic equation is simple and straightforward. Nevertheless, it does not provide much insight into the equation's dynamical meaning (in terms of biological processes). The following derivation is more complex mathematically but it does provide a better understanding of what the logistic means, biologically.

We can ask how many individuals will be in the population at time $t + 1$, given a certain number at time t , the way in which the exponential was introduced. In a perfect density-independent situation we of course have the exponential equation

$$N(t) = N(0)e^{rt}$$

Let $t = 1$ and we obtain

$$N(1) = N(0)e^r$$

Let $t = 2$ and we obtain

$$N(2) = N(0)e^{r^2}$$

But we see that $e^r = N(1)/N(0)$, so that

$$N(2) = N(0)e^r e^r = N(0)e^r (N(1)/N(0))$$

$$N(2) = N(1)e^r,$$

and, in general,

$$N(t + 1) = N(t)e^r = N(t)\lambda$$

where we have written λ in place of e^r . In this equation, it will be recalled, the only things we have assumed about the population is that it reproduces itself and that the rates of birth and death are invariant with respect to changing population density.

Such are the assumptions of density independence. To modify the exponential equation in this form we must postulate or speculate about the form that the density dependence will take. Just as it was necessary to postulate a specific form for $f(N)$ in the derivation of the differential logistic equation so must we postulate a way in which density will affect the production of $N(t + 1)$ by $N(t)$.

Suppose we have 10 individuals in the population at $t = 0$ and at $t = 1$ we get 20; that is, the population is doubled [$N(1) = 2N(0)$]. Suppose also that instead of going from $N(1) = 20$ to $N(2) = 40$ (as we would expect from the exponential law) the population goes only from $N(1) = 20$ to $N(2) = 30$; that is, it increases by a third [$N(2) = 1.5N(1)$]. The “apparent” value of λ went from 2 to 1.5 by the addition to 10 individuals to the population. We might postulate that each individual introduced into the population reduces the apparent λ by a factor of $(2 - 1.5)/10 = 0.05$. Accepting the postulate that each individual introduced into the population reduces the apparent λ by some particular constant fraction, we find that the apparent value [$\lambda'(N)$] must be that constant fraction of the density independent value

$$\lambda'(N) = \frac{1}{C} \lambda$$

and that it must be reduced by some amount by every new individual added to the population. Therefore C must equal 1 when $N = 0$ [$\lambda'(N_0) = \lambda$] and C must increase by some constant factor as $N(t)$ increases (we assume that each individual decreases λ by a constant factor). Thus we have $c = 1 + a N(t)$, which, applied to the above equation, yields

$$\lambda'(N) = \frac{1}{1 + a N(t)} \lambda$$

and the old exponential equation becomes $N(t + 1) = \lambda'(N) N(t)$ or

$$N(t + 1) = \frac{N(t)}{1 + a N(t)} \lambda \quad (8)$$

When the population reaches its carrying capacity, we have

$$K = \frac{\lambda K}{1 + aK}$$

$$1 + aK = \lambda$$

$$a = \frac{\lambda - 1}{K}$$

Equation 8 then becomes

$$N(t + 1) = \frac{\lambda N(t)}{1 + [(\lambda - 1)/K]N(t)} \quad (9)$$

In fact, equation 9 is equivalent to equation 7, as shown below. Also of note, however, is that equation 9 is frequently important practically in computing projected population histories. Next consider equation 9 with $t = 0$.

$$N(1) = \frac{\lambda N_0}{1 + [(\lambda - 1)/K]N_0} \quad [N_0 = N(0)]$$