# MATHEMATICAL MODELS IN BIOLOGY
# AN INTRODUCTION

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CAMBRIDGE
UNIVERSITY PRESS

PUBLISHED BY THE PRESS SYNDICATE OF THE UNIVERSITY OF CAMBRIDGE
The Pitt Building, Trumpington Street, Cambridge, United Kingdom

CAMBRIDGE UNIVERSITY PRESS
The Edinburgh Building, Cambridge CB2 2RU, UK
40 West 20th Street, New York, NY 10011-4211, USA
477 Williamstown Road, Port Melbourne, VIC 3207, Australia
Ruiz de Alarcón 13, 28014 Madrid, Spain
Dock House, The Waterfront, Cape Town 8001, South Africa

http://www.cambridge.org

First published 2004

Printed in the United States of America

*Typeface* Times 10.25/13 pt. *System* $\LaTeX\,2_{\varepsilon}$ [TB]

*A catalog record for this book is available from the British Library.*

*Library of Congress Cataloging in Publication Data*
Allman, Elizabeth Spencer, 1965–
Mathematical models in biology : an introduction / Elizabeth S. Allman, John A. Rhodes.
p. cm.
Includes bibliographical references (p. ).
ISBN 0-521-81980-6 (hb.) – ISBN 0-521-52586-1 (pbk.)
1. Biology – Mathematical models. I. Rhodes, John A. (John Anthony), 1960– II. Title.
QH323.5.A44 2003
570′.1′5118 – dc21 2003043929

ISBN 0 521 81980 6 hardback
ISBN 0 521 52586 1 paperback

# Contents

# 1

# Dynamic Modeling with Difference Equations

Whether we investigate the growth and interactions of an entire population, the evolution of DNA sequences, the inheritance of traits, or the spread of disease, biological systems are marked by change and adaptation. Even when they appear to be constant and stable, it is often the result of a balance of tendencies pushing the systems in different directions. A large number of interactions and competing tendencies can make it difficult to see the full picture at once.

How can we understand systems as complicated as those arising in the biological sciences? How can we test whether our supposed understanding of the key processes is sufficient to describe how a system behaves? Mathematical language is designed for precise description, and so describing complicated systems often requires a *mathematical model.*

In this text, we look at some ways mathematics is used to model dynamic processes in biology. Simple formulas relate, for instance, the population of a species in a certain year to that of the following year. We learn to understand the consequences an equation might have through mathematical analysis, so that our formulation can be checked against biological observation. Although many of the models we examine may at first seem to be gross simplifications, their very simplicity is a strength. Simple models show clearly the implications of our most basic assumptions.

We begin by focusing on modeling the way populations grow or decline over time. Since mathematical models should be driven by questions, here are a few to consider: Why do populations sometimes grow and sometimes decline? Must populations grow to such a point that they are unsustainably large and then die out? If not, must a population reach some equilibrium? If an equilibrium exists, what factors are responsible for it? Is such an equilibrium so delicate that any disruption might end it? What determines whether a given population follows one of these courses or another?

To begin to address these questions, we start with the simplest mathematical model of a changing population.

## 1.1. The Malthusian Model

Suppose we grow a population of some organism, say flies, in the laboratory. It seems reasonable that, on any given day, the population will change due to new births, so that it increases by the addition of a certain multiple $f$ of the population. At the same time, a fraction $d$ of the population will die.

Even for a human population, this model might apply. If we assume humans live for 70 years, then we would expect that from a large population roughly $1/70$ of the population will die each year; so, $d = 1/70$. If, on the other hand, we assume there are about four births in a year for every hundred people, we have $f = 4/100$. Note that we have chosen *years* as units of time in this case.

- ► Explain why, for any population, $d$ must be between 0 and 1. What would $d < 0$ mean? What would $d > 1$ mean?
- ► Explain why $f$ must be at least 0, but could be bigger than 1. Can you name a real organism (and your choice of units for time) for which $f$ would be bigger than 1?
- ► Using *days* as your unit of time, what values of $f$ and $d$ would be in the right ballpark for elephants? Fish? Insects? Bacteria?

To track the population $P$ of our laboratory organism, we focus on $\Delta P$, the *change* in population over a single day. So, in our simple conception of things,

$$\Delta P = fP - dP = (f - d)P.$$

What this means is simply that given a current population $P$, say $P = 500$, and the fecundity and death rates $f$ and $d$, say $f = .1$ and $d = .03$, we can predict the change in the population $\Delta P = (.1 - .03)500 = 35$ over a day. Thus, the population at the beginning of the next day is $P + \Delta P = 500 + 35 = 535$.

Some more notation will make this simpler. Let

$$P_t = P(t) = \text{the size of the population measured on day } t,$$

so

$$\Delta P = P_{t+1} - P_t$$

Table 1.1. *Population Growth According to a Simple Model*

| Day | Population |
|---|---|
| 0 | 500 |
| 1 | $(1.07)500 = 535$ |
| 2 | $(1.07)^2 500 = 572.45$ |
| 3 | $(1.07)^3 500 \approx 612.52$ |
| 4 | $(1.07)^4 500 \approx 655.40$ |
| $\vdots$ | $\vdots$ |

is the *difference* or change in population between two consecutive days. (If you think there should be a subscript $t$ on that $\Delta P$, because $\Delta P$ might be different for different values of $t$, you are right. However, it's standard practice to leave it off.)

Now what we ultimately care about is understanding the population $P_t$, not just $\Delta P$. But

$$P_{t+1} = P_t + \Delta P = P_t + (f - d)P_t = (1 + f - d)P_t.$$

Lumping some constants together by letting $\lambda = 1 + f - d$, our model of population growth has become simply

$$P_{t+1} = \lambda P_t.$$

Population ecologists often refer to the constant $\lambda$ as the *finite growth rate* of the population. (The word "finite" is used to distinguish this number from any sort of instantaneous rate, which would involve a derivative, as you learn in calculus.)

For the values $f = .1$, $d = .03$, and $P_0 = 500$ used previously, our entire model is now

$$P_{t+1} = 1.07P_t, \quad P_0 = 500.$$

The first equation, relating $P_{t+1}$ and $P_t$, is referred to as a *difference equation* and the second, giving $P_0$, is its *initial condition.* With the two, it is easy to make a table of values of the population over time, as in Table 1.1.

From Table 1.1, it's even easy to recognize an explicit formula for $P_t$,

$$P_t = 500(1.07)^t.$$

For this model, we can now easily predict populations at any future times.

It may seem odd to call $P_{t+1} = (1 + f - d)P_t$ a difference equation, when the difference $\Delta P$ does not appear. However, the equations

$$P_{t+1} = (1 + f - d)P_t$$

and

$$\Delta P = (f - d)P$$

are mathematically equivalent, so either one is legitimately referred to by the same phrase.

**Example.** Suppose that an organism has a very rigid life cycle (which might be realistic for an insect), in which each female lays 200 eggs, then all the adults die. After the eggs hatch, only 3% survive to become adult females, the rest being either dead or males. To write a difference equation for the females in this population, where we choose to measure $t$ in generations, we just need to observe that the death rate is $d = 1$, while the effective fecundity is $f = .03(200) = 6$. Therefore,

$$P_{t+1} = (1 + 6 - 1)P_t = 6P_t.$$

- ► Will this population grow or decline?
- ► Suppose you don't know the effective fecundity, but do know that the population is stable (unchanging) over time. What must the effective fecundity be? (*Hint*: What is $1 + f - d$ if the population is stable?) If each female lays 200 eggs, what fraction of them must hatch and become females?

Notice that in this last model we ignored the males. This is actually a quite common approach to take and simplifies our model. It does mean we are making some assumptions, however. For this particular insect, the precise number of males may have little effect on how the population grows. It might be that males are always found in roughly equal numbers to females so that we know the total population is simply double the female one. Alternately, the size of the male population may behave differently from the female one, but whether there are few males or many, there are always enough that female reproduction occurs in the same way. Thus, the female population is the important one to track to understand the long-term growth or decline of the population.

- ► Can you imagine circumstances in which ignoring the males would be a bad idea?

**What is a difference equation?** Now that you have seen a difference equation, we can attempt a definition: a difference equation is a formula expressing values of some quantity $Q$ in terms of previous values of $Q$. Thus, if $F(x)$ is any function, then

$$Q_{t+1} = F(Q_t)$$

is called a difference equation. In the previous example, $F(x) = \lambda x$, but often $F$ will be more complicated.

In studying difference equations and their applications, we will address two main issues: 1) How do we find an appropriate difference equation to model a situation? 2) How do we understand the behavior of the difference equation model once we have found it?

Both of these things can be quite hard to do. You learn to model with difference equations by looking at ones other people have used and then trying to create some of your own. To be honest, though, this will not necessarily make facing a new situation easy. As for understanding the behavior a difference equation produces, usually we cannot hope to find an explicit formula like we did for $P_t$ describing the insect population. Instead, we develop techniques for getting less precise qualitative information from the model.

The particular difference equation discussed in this section is sometimes called an *exponential* or *geometric model*, since the model results in exponential growth or decay. When applied to populations in particular, it is associated with the name of Thomas Malthus. Mathematicians, however, tend to focus on the form of the equation $P_{t+1} = \lambda P_t$ and say the model is *linear*. This terminology can be confusing at first, but it will be important; *a linear model produces exponential growth or decay.*

## Problems

1.1.1. A population is originally 100 individuals, but because of the combined effects of births and deaths, it triples each hour.

   a. Make a table of population size for $t = 0$ to 5, where $t$ is measured in hours.

   b. Give two equations modeling the population growth by first expressing $P_{t+1}$ in terms of $P_t$ and then expressing $\Delta P$ in terms of $P_t$.

   c. What, if anything, can you say about the birth and death rates for this population?

1.1.2. In the early stages of the development of a frog embryo, cell division occurs at a fairly regular rate. Suppose you observe that all cells divide, and hence the number of cells doubles, roughly every half-hour.

a. Write down an equation modeling this situation. You should specify how much real-world time is represented by an increment of 1 in $t$ and what the initial number of cells is.
b. Produce a table and graph of the number of cells as a function of $t$.
c. Further observation shows that, after 10 hours, the embryo has around 30,000 cells. Is this roughly consistent with your model? What biological conclusions and/or questions does this raise?

1.1.3. Using a hand calculator, make a table of population values at times 0 through 6 for the following population models. Then graph the tabulated values.

a. $P_{t+1} = 1.3P_t$, $P_0 = 1$
b. $N_{t+1} = .8N_t$, $N_0 = 10$
c. $\Delta Z = .2Z$, $Z_0 = 10$

1.1.4. Redo Problem 1.1.3(a) using MATLAB by entering a command sequence like:

```
p=1
x=p
p=1.3*p
x=[x p]
p=1.3*p      (Because this repeats an earlier command, you can save
x=[x p]      some typing by hitting the "↑" key twice.)
 ⋮
```

Explain how this works.

Now redo the problem again by a command sequence like:

```
p=1
x=1
for i=1:10
    p=1.3*p      (The indentation is not necessary, but helps make
    x=[x p]      the for-end loop clearer to read.)
end
```

Explain how this works as well.

Graph your data with:

```
plot([0:10],x)
```

1.1.5. For the model in Problem 1.1.3(a), how much time must pass before the population exceeds 10, exceeds 100, and exceeds 1,000? (Use MATLAB to do this experimentally, and then redo it using logarithms and the fact that $P_t = 1.3^t$.) What do you notice about the difference between these times? Explain why this pattern holds.

1.1.6. If the data in Table 1.2 on population size were collected in a laboratory experiment using insects, would it be consistent with a geometric model? Would it be consistent with a geometric model for at least some range of times? Explain.

1.1.7. Complete the following:

a. The models $P_t = kP_{t-1}$ and $\Delta P = rP$ represent *growing* populations when $k$ is any number in the range ___ and when $r$ is any number in the range ___.

b. The models $P_t = kP_{t-1}$ and $\Delta P = rP$ represent *declining* populations when $k$ is any number in the range ___ and when $r$ is any number in the range ___.

c. The models $P_t = kP_{t-1}$ and $\Delta P = rP$ represent *stable* populations when $k$ is any number in the range ___ and when $r$ is any number in the range ___.

1.1.8. Explain why the model $\Delta Q = rQ$ cannot be biologically meaningful for describing a population when $r < -1$.

1.1.9. Suppose a population is described by the model $N_{t+1} = 1.5N_t$ and $N_5 = 7.3$. Find $N_t$ for $t = 0, 1, 2, 3,$ and 4.

1.1.10. A model is said to have a *steady state* or *equilibrium point* at $P^*$ if whenever $P_t = P^*$, then $P_{t+1} = P^*$ as well.

a. Rephrase this definition as: A model is said to have a *steady state* at $P^*$ if whenever $P = P^*$, then $\Delta P = \ldots.$

b. Rephrase this definition in more intuitive terms: A model is said to have a *steady state* at $P^*$ if ....

c. Can a model described by $P_{t+1} = (1 + r)P_t$ have a steady state? Explain.

Table 1.2. *Insect Population Values*

| $t$ | 0 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 |
|---|---|---|---|---|---|---|---|---|---|---|---|
| $P_t$ | .97 | 1.52 | 2.31 | 3.36 | 4.63 | 5.94 | 7.04 | 7.76 | 8.13 | 8.3 | 8.36 |

Table 1.3. *U.S. Population Estimates*

| Year | Population (in 1,000s) |
|---|---|
| 1920 | 106,630 |
| 1925 | 115,829 |
| 1930 | 122,988 |
| 1935 | 127,252 |
| 1940 | 131,684 |
| 1945 | 131,976 |
| 1950 | 151,345 |
| 1955 | 164,301 |
| 1960 | 179,990 |

1.1.11. Explain why the model $\Delta P = rP$ leads to the formula $P_t = (1 + r)^t P_0$.

1.1.12. Suppose the size of a certain population is affected only by birth, death, immigration, and emigration – each of which occurs in a yearly amount proportional to the size of a population. That is, if the population is $P$, within a time period of 1 year, the number of births is $bP$, the number of deaths is $dP$, the number of immigrants is $iP$, and the number of emigrants is $eP$, for some $b,\ d,\ i,$ and $e$. Show the population can still be modeled by $\Delta P = rP$ and give a formula for $r$.

1.1.13. As limnologists and oceanographers are well aware, the amount of sunlight that penetrates to various depths of water can greatly affect the communities that live there. Assuming the water has uniform *turbidity*, the amount of light that penetrates through a 1-meter column of water is proportional to the amount entering the column.

a. Explain why this leads to a model of the form $L_{d+1} = kL_d$, where $L_d$ denotes the amount of light that has penetrated to a depth of $d$ meters.

b. In what range must $k$ be for this model to be physically meaningful?

c. For $k = .25,\ L_0 = 1$, plot $L_d$ for $d = 0, 1, \ldots, 10$.

d. Would a similar model apply to light filtering through the canopy of a forest? Is the "uniform turbidity" assumption likely to apply there?

1.1.14. The U.S. population data in Table 1.3 is from (Keyfitz and Flieger, 1968).

a. Graph the data. Does this data seem to fit the geometric growth model? Explain why or why not using graphical and numerical evidence. Can you think of factors that might be responsible for any deviation from a geometric model?

b. Using the data only from years 1920 and 1925 to estimate a growth rate for a geometric model, see how well the model's results agree with the data from subsequent years.

c. Rather than just using 1920 and 1925 data to estimate a growth parameter for the U.S. population, find a way of using all the data to get what (presumably) should be a better geometric model. (Be creative. There are several reasonable approaches.) Does your new model fit the data better than the model from part (b)?

1.1.15. Suppose a population is modeled by the equation $N_{t+1} = 2N_t$, when $N_t$ is measured in *individuals*. If we choose to measure the population in *thousands of individuals*, denoting this by $P_t$, then the equation modeling the population *might* change. Explain why the model is still just $P_{t+1} = 2P_t$. (*Hint*: Note that $N_t = 1000P_t$.)

1.1.16. In this problem, we investigate how a model must be changed if we change the amount of time represented by an increment of 1 in the time variable $t$. It is important to note that this is not always a biologically meaningful thing to do. For organisms like certain insects, generations do not overlap and reproduction times are regularly spaced, so using a time increment of less than the span between two consecutive birth times would be meaningless. However, for organisms like humans with overlapping generations and continual reproduction, there is no natural choice for the time increment. Thus, these populations are sometimes modeled with an "infinitely small" time increment (i.e., with differential equations rather than difference equations). This problem illustrates the connection between the two types of models.

A population is modeled by $N_{t+1} = 2N_t$, $N_0 = A$, where each increment of $t$ by 1 represents a passage of 1 year.

a. Suppose we want to produce a new model for this population, where each time increment of $t$ by 1 now represents 0.5 years, and the population size is now denoted $P_t$. We want our new model to produce the same populations as the first model at 1-year intervals (so $P_{2t} = N_t$). Thus, we have Table 1.4. Complete the table for $P_t$ so that the growth is still geometric. Then give an equation of the model relating $P_{t+1}$ to $P_t$.

b. Produce a new model that agrees with $N_t$ at 1-year intervals, but denote the population size by $Q_t$, where each time increment of

Table 1.4. *Changing Time Steps in a Model*

| $t$ | 0 |  | 1 |  | 2 |  | 3 |
|---|---|---|---|---|---|---|---|
| $N_t$ | A |  | 2A |  | 4A |  | 8A |
| $t$ | 0 | 1 | 2 | 3 | 4 | 5 | 6 |
| $P_t$ | A |  | 2A |  | 4A |  | 8A |

$t$ by 1 represents 0.1 years (so, $Q_{10t} = N_t$). You should begin by producing tables similar to those in part (a).

c. Produce a new model that agrees with $N_t$ at 1-year intervals, but denote the population size by $R_t$, where each time increment of $t$ by 1 represents $h$ years (so $R_{\frac{1}{h}t} = N_t$). ($h$ might be either bigger or smaller than 1; the same formula describes either situation.)

d. Generalize parts (a–c), writing a paragraph to explain why, if our original model uses a time increment of 1 year and is given by $N_{t+1} = kN_t$, then a model producing the same populations at 1-year intervals, but that uses a time increment of $h$ years, is given by $P_{t+1} = k^h P_t$.

e. (Calculus) If we change the name of the time interval $h$ to $\Delta t$, part (d) shows that

$$\frac{\Delta P}{\Delta t} = \frac{k^h - 1}{h} P.$$

If $\Delta t = h$ is allowed to become *infinitesimally small*, this means

$$\frac{dP}{dt} = \lim_{h \to 0} \frac{k^h - 1}{h} P.$$

Illustrate that

$$\lim_{h \to 0} \frac{k^h - 1}{h} = \ln k$$

by choosing a few values of $k$ and a very small $h$ and comparing the values of $\ln k$ and $\frac{k^h - 1}{h}$.

This result is formally proved by:

$$\lim_{h \to 0} \frac{k^h - 1}{h} = \lim_{h \to 0} \frac{k^{0+h} - k^0}{h} = \frac{d}{dx} k^x \bigg|_{x=0} = \ln k \, k^x \big|_{x=0} = \ln k.$$

f. (Calculus) Show the solution to $\frac{dP}{dt} = \ln k P$ with initial value $P(0) = P_0$ is

$$P(t) = P_0 e^{t \ln k} = P_0 k^t.$$

How does this compare to the formula for $N_t$, in terms of $N_0$ and $k$, for the difference equation model $N_{t+1} = kN_t$? Ecologists often refer to the $k$ in either of these formulas as the *finite growth rate* of the population, while $\ln k$ is referred to as the *intrinsic growth rate*.

## 1.2. Nonlinear Models

The Malthusian model predicts that population growth will be exponential. However, such a prediction cannot really be accurate for very long. After all, exponential functions grow quickly and without bound; and, according to such a model, sooner or later there will be more organisms than the number of atoms in the universe. The model developed in the last section must be overlooking some important factor. To be more realistic in our modeling, we need to reexamine the assumptions that went into that model.

The main flaw is that we have assumed the fecundity and death rates for our population are the same regardless of the size of the population. In fact, when a population gets large, it might be more reasonable to expect a higher death rate and a lower fecundity. Combining these factors, we could say that, as the population size increases, the finite growth rate should decrease. We need to somehow modify our model so that the growth rate depends on the size of the population; that is, the growth rate should be *density dependent*.

- ► What biological factors might be the cause of the density dependence? Why might a large population have an increased death rate and/or decreased birth rate?

**Creating a nonlinear model.** To design a better model, it's easiest to focus on $\dfrac{\Delta P}{P}$, the change in population per individual, or the *per-capita growth rate* over a single time step. Once we have understood the per-capita growth rate and found a formula to describe it, we will be able to obtain a formula for $\Delta P$ from that.

For small values of $P$, the per-capita growth rate should be large, since we imagine a small population with lots of resources available in its environment to support further growth. For large values of $P$, however, per-capita growth should be much smaller, as individuals compete for both food and space. For even larger values of $P$, the per-capita growth rate should be negative, since that would mean the population will decline. It is reasonable then to assume $\Delta P/P$, as a function of $P$, has a graph something like that in Figure 1.1.

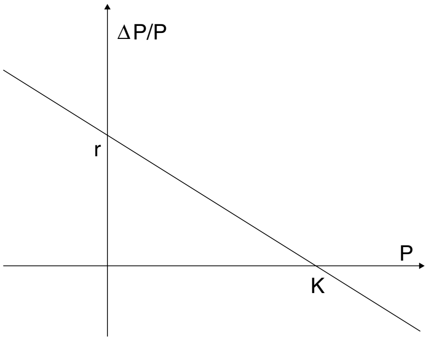

Figure 1.1. Per-capita growth rate as a function of population size.

Of course we cannot say exactly what a graph of $\Delta P/P$ should look like without collecting some data. Perhaps the graph should be concave for instance. However, this is a good first attempt at creating a better model.

► Graph the per-capita growth rate for the Malthusian model. How is your graph different from Figure 1.1?

For the Malthusian model $\Delta P/P = r$, so that the graph of the per-capita growth rate is a horizontal line – there is no decrease in $\Delta P/P$ as $P$ increases.

In contrast, the sloping line of Figure 1.1 for an improved model leads to the formula $\Delta P/P = mP + b$, for some $m < 0$ and $b > 0$. It will ultimately be clearer to write this as

$$\frac{\Delta P}{P} = r\left(1 - \frac{P}{K}\right)$$

so that $K$ is the horizontal intercept of the line, and $r$ is the vertical intercept. Note that both $K$ and $r$ should be positive. With a little algebra, we get

$$P_{t+1} = P_t\left(1 + r\left(1 - \frac{P_t}{K}\right)\right)$$

as our difference equation. This model is generally referred to as the *discrete logistic model*, though, unfortunately, other models also go by that name as well.

The parameters $K$ and $r$ in our model have direct biological interpretations. First, if $P < K$, then $\Delta P/P > 0$. With a positive per-capita growth rate, the population will increase. On the other hand, if $P > K$, then $\Delta P/P < 0$. With a negative per-capita growth rate, the population will decrease. $K$ is therefore called the *carrying capacity* of the environment, because it represents the maximum number of individuals that can be supported over a long period.

However, when the population is small (i.e., $P$ is much smaller than $K$), the factor $(1 - P/K)$ in the per-capita growth rate should be close to 1. Therefore, for small values of $P$, our model is approximately

$$P_{t+1} \approx (1+r)P_t.$$

In other words, $r$ plays the role of $f - d$, the fecundity minus the death rate, in our earlier linear model. The parameter $r$ simply reflects the way the population would grow or decline in the absence of density-dependent effects – when the population is far below the carrying capacity. The standard terminology for $r$ is that it is the *finite intrinsic growth rate*. "Intrinsic" refers to the absence of density-dependent effects, whereas "finite" refers to the fact that we are using time steps of finite size, rather than the infinitesimal time steps of a differential equation.

► What are ballpark figures you might expect for $r$ and $K$, assuming you want to model your favorite species of fish in a small lake using a time increment of 1 year?

As you will see in the problems, there are many ways different authors choose to write the logistic model, depending on whether they look at $\Delta P$ or $P_{t+1}$ and whether they multiply out the different factors. A key point to help you recognize this model is that both $\Delta P$ and $P_{t+1}$ are expressed as quadratic polynomials in terms of $P_t$. Furthermore, these polynomials have no constant term (i.e., no term of degree zero in $P$). Thus, the logistic model is about the simplest nonlinear model we could develop.

**Iterating the model.** As with the linear model, our first step in understanding this model is to choose some particular values for the parameters $r$ and $K$, and for the initial population $P_0$, and compute future population values. For example, choosing $K$ and $r$ so that $P_{t+1} = P_t(1 + .7(1 - P_t/10))$ and $P_0 = 0.4346$, we get Table 1.5.

► How can it make sense to have populations that are not integers?

Table 1.5. *Population Values from a Nonlinear Model*

| $t$ | 0 | 1 | 2 | 3 | 4 | 5 | 6 |
|---|---|---|---|---|---|---|---|
| $P_t$ | .4346 | .7256 | 1.1967 | 1.9341 | 3.0262 | 4.5034 | 6.2362 |
| $t$ | 7 | 8 | 9 | 10 | 11 | 12 | ... |
| $P_t$ | 7.8792 | 9.0489 | 9.6514 | 9.8869 | 9.9652 | 9.9895 | ... |

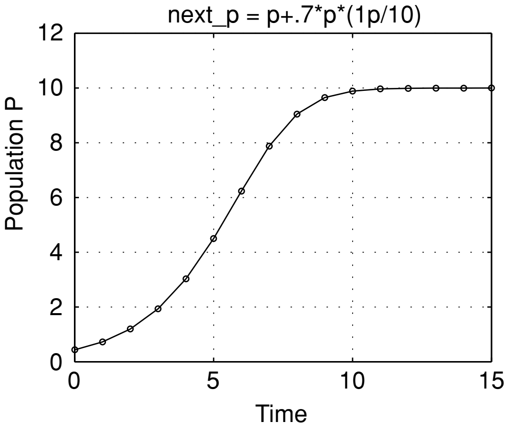

Figure 1.2. Population values from a nonlinear model.

If we measure population size in units such as thousands, or millions of individuals, then there is no reason for populations to be integers. For some species, such as commercially valuable fish, it might even be appropriate to use units of mass or weight, like tons.

Another reason that noninteger population values are not too worrisome, even if we use units of individuals, is that we are only attempting to approximately describe a population's size. We do not expect our model to give exact predictions. As long as the numbers are large, we can just ignore fractional parts without a significant loss.

In the table, we see the population increasing toward the carrying capacity of 10 as we might have expected. At first this increase seems slow, then it speeds up and then it slows again. Plotting the population values in Figure 1.2 shows the sigmoid-shaped pattern that often appears in data from carefully controlled laboratory experiments in which populations increase in a limited environment. (The plot shows the population values connected by line segments to make the pattern clearer, even though the discrete time steps of our model really give populations only at integer times.) Biologically, then, we have made some progress; we have a more realistic model to describe population growth.

Mathematically, things are not so nice, though. Unlike with the linear model, there is no obvious formula for $P_t$ that emerges from our table. In fact, the only way to get the value of $P_{100}$ seems to be to create a table with a hundred entries in it. We have lost the ease with which we could predict future populations.

This is something we simply have to learn to live with: Although nonlinear models are often more realistic models to use, we cannot generally get explicit formulas for solutions to nonlinear difference equations. Instead, we must rely more on graphical techniques and numerical experiments to give us insight into the models' behaviors.

**Cobwebbing.** Cobwebbing is the basic graphical technique for understanding a model such as the discrete logistic equation. It's best illustrated by an example. Consider again the model

$$P_0 = 2.3, \quad P_{t+1} = P_t\left(1 + .7\left(1 - \frac{P_t}{10}\right)\right).$$

Begin by graphing the parabola defined by the equation giving $P_{t+1}$ in terms of $P_t$, as well as the diagonal line $P_{t+1} = P_t$, as shown in Figure 1.3. Since the population begins at $P_0 = 2.3$, we mark that on the graph's horizontal axis. Now, to find $P_1$, we just move vertically upward to the graph of the parabola to find the point $(P_0, P_1)$, as shown in the figure.

We would like to find $P_2$ next, but to do that we need to mark $P_1$ on the horizontal axis. The easiest way to do that is to move horizontally from the point $(P_0, P_1)$ toward the diagonal line. When we hit the diagonal line, we will be at $(P_1, P_1)$, since we've kept the same second coordinate, but changed the first coordinate. Now, to find $P_2$, we just move vertically back

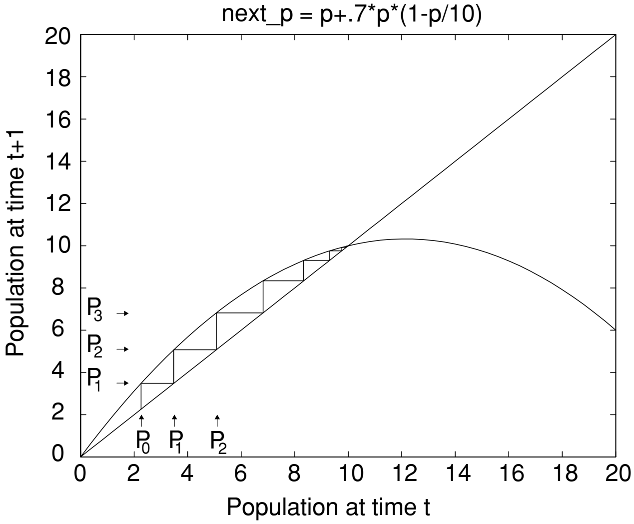

Figure 1.3. Cobweb plot of a nonlinear model.

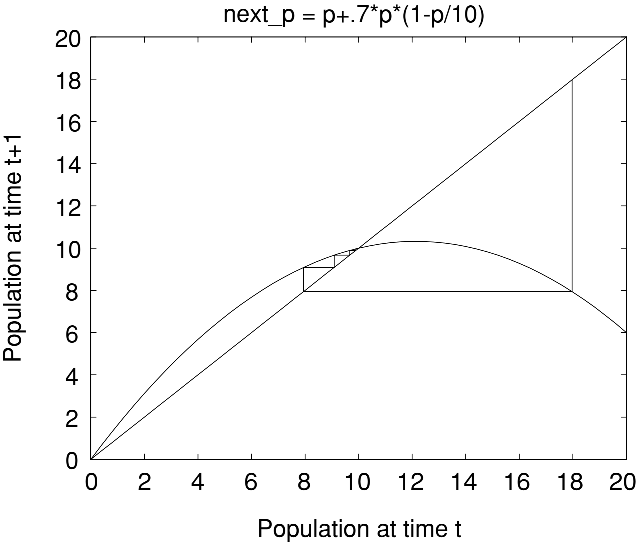

Figure 1.4. Cobweb plot of a nonlinear model.

to the parabola to find the point $(P_1, P_2)$. Now it's just a matter of repeating these steps forever: Move vertically to the parabola, then horizontally to the diagonal line, then vertically to the parabola, then horizontally to the diagonal line, and so on.

It should be clear from this graph that if the initial population $P_0$ is anything between 0 and $K = 10$, then the model with $r = .7$ and $K = 10$ will result in an always increasing population that approaches the carrying capacity.

If we keep the same values of $r$ and $K$, but let $P_0 = 18$, the cobweb looks like that in Figure 1.4.

Indeed, it becomes clear that if $P_0$ is any value above $K = 10$, then we see an immediate drop in the population. If this drop is to a value below the carrying capacity, there will then be a gradual increase back toward the carrying capacity.

- ► Find the positive population size that corresponds to where the parabola crosses the horizontal axis for the model $P_{t+1} = P_t(1 + .7(1 - P_t/10))$ by setting $P_{t+1} = 0$.
- ► What happens if $P_0$ is higher than the value you found in the last question?

If the population becomes negative, then we should interpret that as extinction.