1

Introduction

1.1 What is population biology?

A *population* is a group of individuals of the same species that have a high probability of interacting with each other. A simple example would be trout in a lake, or moose on Isle Royale, although in many cases the boundaries delineating a population are not as clear cut. Population biology is simply the study of biological populations.

Why study population biology? An understanding of complex ecological communities with numerous species interacting with each other and the environment requires an understanding of the simpler ecological systems of one or two species first. We will begin by focusing on the population biology of a single species for two reasons. First, an understanding of the dynamics of a single species leads to the primary questions of population ecology. Second, this is the simplest system that can be studied from a population approach.

Why do we focus on numbers of individuals as the variable of interest, rather than a variable like energy flow? We do this because it is possible, even likely, that small numbers of individuals may have effects, especially on population stability, out of

Population biology includes genetic and evolutionary questions; it is broader than population ecology.

Although population ecology might strictly refer to a single species, we use it in this text more broadly to refer to studies focusing on numbers within a species and explicitly consider one or two species at a time.

Here 'regulating' means controlling the population growth.

proportion to their numbers. For example, a small popuation of predators may play a major role in regulating a prey population with a large population size. Diseases, ranging from AIDS to the plague, may have extreme effects on the dynamics of the host populations.

Population biology is by its nature a science that focuses on numbers. Thus, we will be interested in understanding, explaining, and predicting changes in the size of populations. Several intriguing patterns of population change through time are illustrated in Figure 1.1. What causes these different patterns to appear? The answer to this question is a central theme of this book.

1.2   Role of models in population biology

Answering many important questions in conservation biology requires the use of models from population biology.

We do not address the important issues of population estimation or experimental design in this book.

The goals of population biology are to understand and predict the dynamics of populations. Understanding, explaining, and predicting dynamics of biological populations will require models, models that are expressed in the language of mathematics. In this book, we emphasize the role of models in understanding population biology. Mathematical models are essential in making precise theoretical arguments about the factors affecting the rate of change of population size.

A full appreciation of the role of models will come as you progress through the book, but a few preliminary observations on how models are employed are very useful. First, a model cannot be shown to be true by a single experiment. However, a model can be shown to be false by a single experiment that does not agree with the predictions of the model. What does it mean to say that a model is false? Assuming that no logical (or mathematical) mistakes have been made, it means that one of the assumptions of the model is not met by the natural system examined. This can be a very useful result, in that it indicates where empirical work should concentrate. In the next chapter we will see just this approach, in elucidating the central question in population biology: *What prevents uncontrolled population growth?*
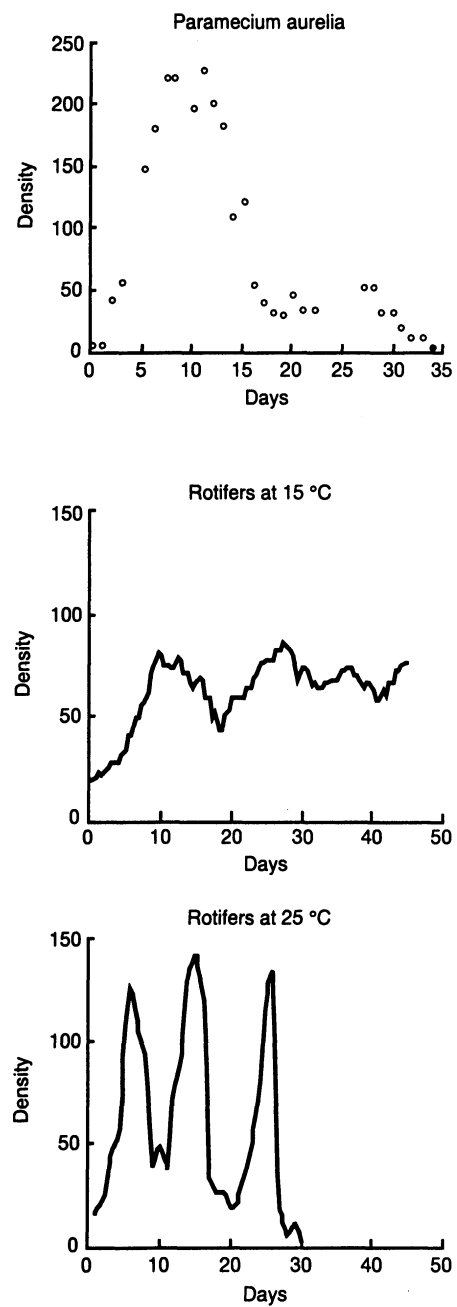
FIGURE 1.1. Three examples of population dynamics from the laboratory. The top example is from Gause (1935); the bottom two are dynamics of rotifers at two different temperatures from Halbach (1979).

1.3 Some successful models in population biology

What are some examples of models that have proven successful in population biology? We provide two brief examples here, one of which we will cover in the text, and one that is beyond the scope of the this book.

One of the most successful theories in population biology has been that of the *dynamics of age–structured population growth*. Given information about the age at which individuals have off-spring and the probabilities of death at different ages, we can make detailed predictions about the long term changes in population numbers. We develop the basics of this theory in the next chapter.

Age–structured population growth has played an important role in the field of conservation biology. We can use this theory to ask what changes in survival of different ages, or changes in birth rates, could make the difference between a population that is increasing and one which is declining. Thus, as in studies of the desert tortoise (Doak et al., 1994), this theory can be used to make suggestions that will help in developing a plan to promote the long–term survival of an endangered species.

A second example of successful theory in population biology is the *theory of spatial spread*. As illustrated in Figure 1.2, we can predict the future rate of spread of some populations from initial observations. (Explaining why this is true is beyond the scope of this book.)

Being able to predict the rate of spread of organisms is of great practical importance. For example, the ability to predict the rate of spread of an undesirable species, such as the Africanized honey-bee, can help in making preparations for dealing with difficulties caused by this invader. Understanding the rate of spread may also help in the design of control measures to reduce the rate of spread of pests.

These are just two examples of how theory can help to understand questions in population biology. Many more examples of this kind will appear throughout the text.
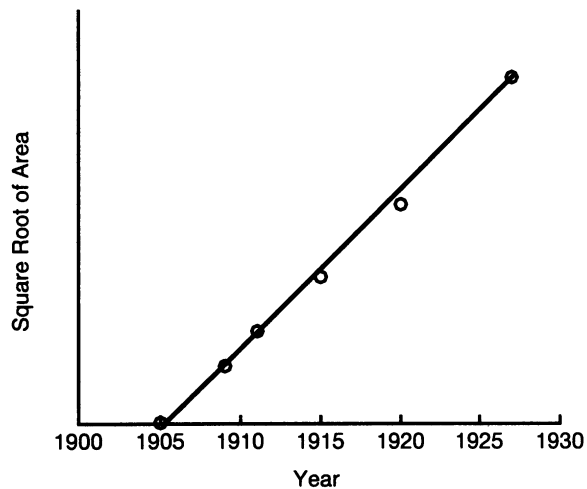
FIGURE 1.2. The rate of spatial spread of the muskrat in central Europe (from Skellam, 1951). As indicated by the straight line (which is fit by eye), the square root of the area occupied by the species increases in an almost perfectly linear manner.

Problems

1. Write a short essay explaining why it is easier to demonstrate that a theory is incorrect than to demonstrate that a theory is correct.

2. Write a short essay explaining the value of theories that can be shown to be incorrect.

Suggestions for further reading

Kingsland (1985) has written a history of population ecology. Virtually any text in ecology will help provide further insight into some of the issues raised here.

A classic paper on the role of models is Levins (1966). See also Pielou (1981). The book *Perspectives in Ecology* by Roughgarden et al. (1989) has a number of essays on the role of theory.

The book *Dynamics of Invasions* by Hengeveld (1989) provides many examples of spatial spread.

Part I

Single species

2

Density-Independent Population Growth

In this chapter, we examine the simplest models of population growth: those which assume density independence. We say that the growth of a population is *density independent* if the birth and death rates per individual do not depend on the population size. We begin with models that also ignore the effects of age structure, and then move on to include the effects of age structure. We look at both species with overlapping generations, like humans, and those with discrete generations, like many butterflies. The predictions of these models set the stage for the rest of our investigations of population dynamics. The approach we use to set up these models will be used again and again. Additionally, we introduce many of the mathematical tools that are used throughout our investigations.

Later, we will look at density dependence.

2.1   The simplest model of population growth

We first examine the simplest model of population growth of a single species. The model begins with two assumptions of density independence:

As with all models, you should consider the importance of factors we ignore. List some factors we have ignored.

These assumptions correspond to density independence because they imply that the per capita birth and death rates are independent of density.

● The rate of births is proportional to the number of individuals present.

● The rate of deaths is proportional to the number of individuals present.

We will look at two models that incorporate these assumptions: one is for populations where the generations overlap and the second for populations in which the generations are nonoverlapping.

Continuous time

We begin with species in which generations overlap and for which births can occur at any time, as in humans. Then it makes sense to predict or count the population size at all times, rather than at specified intervals. Thus, we will use a *continuous time model*. We also need to think about our measure of population size. In this chapter we typically use the individual as the basic unit of population size and count the total number of individuals. However, in some cases it would be both more convenient and realistic to count *biomass*, the total weight of the population. Although counting the number of individuals in the population means the size of the population must be an integer, we do not restrict the population size N at time t to be an integer. Instead, we assume that describing the population by a continuous variable is a reasonable approximation.

Let b be the birth rate per capita and m (for mortality) the death rate per capita. The rate of change of the total number of individuals, $\frac{dN}{dt}$, is given by the rate of births in the population minus the rate of deaths. The rate of births in the population is given by the per capita birth rate times the number of individuals, or bN. Similarly, the population level death rate is given by mN. Thus

$$\frac{dN}{dt} = bN - mN. \qquad (2.1)$$

This equation is usually written as

$$\frac{dN}{dt} = rN, \qquad (2.2)$$

where $r = b - m$. Note that in this equation the parameter r, the *intrinsic rate of increase*, depends on both the birth rate and the death rate. This model is simple enough that we can solve it completely by finding the population size as a function of time, $N(t)$. We will go through all the steps here because we use a similar process in more complex models. We first separate the variables by putting all the terms with N on one side of the equation and all the terms with t on the other side of the equation:

$$\frac{dN}{N} = r dt. \tag{2.3}$$

Integrate both sides of the equation from $t = 0$ to $t = T$,

Recall that $\int \frac{1}{N} dN = \ln(N)$.

$$\int_{t=0}^{t=T} \frac{dN}{N} = \int_{t=0}^{t=T} r dt. \tag{2.4}$$

Compute the integrals to find

$\ln N(t)|_{t=0}^{t=T}$ means $\ln N(T) - \ln N(0)$.

$$\ln N(t)|_{t=0}^{t=T} = r t|_{t=0}^{t=T}. \tag{2.5}$$

Evaluate the terms in this equation at the specified limits, obtaining

$$\ln(N(T)) - \ln(N(0)) = rT. \tag{2.6}$$

Take the exponential of both sides

$$e^{\ln(N(T))} e^{-\ln(N(0))} = e^{rT}. \tag{2.7}$$

Finally, solve for $N(T)$:

Recall that $e^{\ln(a)} = a$ and $e^{-\ln(a)} = \frac{1}{a}$.

$$\frac{N(T)}{N(0)} = e^{rT} \tag{2.8}$$

$$N(T) = N(0)e^{rT}. \tag{2.9}$$

This model predicts that

- if $r = 0$, the population size is stationary

- if $r > 0$, the population grows exponentially without bound

- if $r < 0$, the population approaches 0.

These dynamics are illustrated in Figure 2.1.

Solve Problem 1.

There are important biological and mathematical conclusions we wish to draw from this simple model. First, the model can
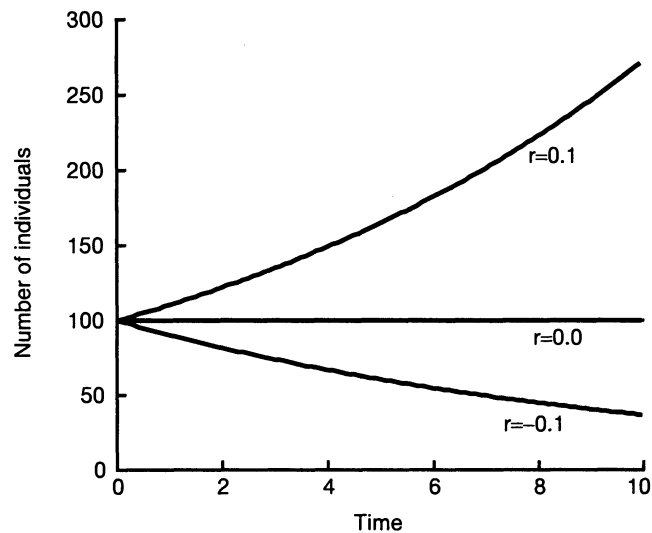
FIGURE 2.1. Dynamics of continuous time population growth.

help answer the question: do biological populations ever demonstrate exponential growth? Yes, but only for short times, because exponential growth is so rapid that populations cannot grow exponentially for long. Second, an equilibrium population is only attained when r is exactly 0, which is clearly an unlikely event. Consequently, populations that remain constant over a prolonged period of time, or even approximately constant, cannot be explained by this model. Thus, the density-independent model cannot explain most populations we see in nature.

The model cannot tell us why a population does not keep growing exponentially, but perhaps you have some ideas.

Third, we will use the exponential solution to the linear growth equation (2.2) many times. Commit to memory the relationship between the sign of r and the fate of the population, as this qualitative conclusion is very important. We emphasize this in the box.

Equation (2.2) is called 'linear' because the right-hand side only has terms that contain N; there are no constant terms and no terms with N raised to a power. Linear equations are special, as we shall see throughout the book.

Discrete time

Is the continuous time model a good choice for all species? Recall our assumption about overlapping generations and births occurring at any time. Butterflies like the bay checkerspot *Euphydrias editha* breed once per year, laying their eggs close to April 1. Adults only fly for a short period, and then die. Large ungulates,

---

Box 2.1. Solution for exponential growth in continuous time.

Here we summarize equation (2.3) - (2.9). The solution to

$$\frac{dN}{dt} = rN$$

is

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

This equation and its solution will be used many times. The *qualitative* behavior of the solution is determined only by the sign of r.

- For $r > 0$, the solution increases without bound,

- for $r = 0$, the solution is a constant, and

- for $r < 0$ the solution approaches zero.
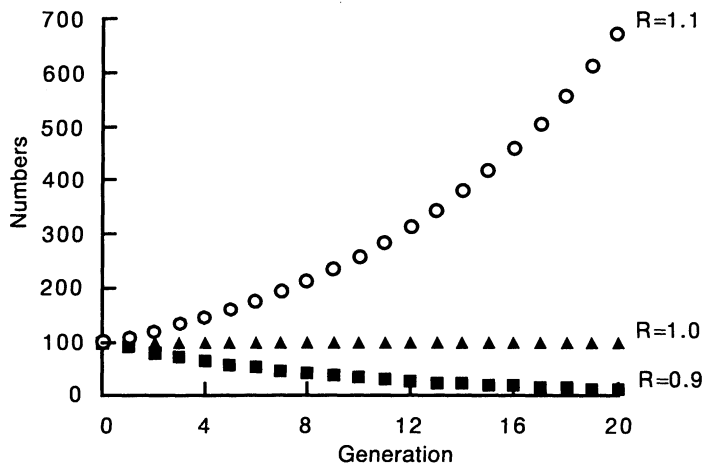

FIGURE 2.2. Dynamics of discrete time population growth.

such as moose, have offspring only once per year in the spring, with adults rarely living more then 10 years. For these species, a model which assumes both that births occur continuously and that generations overlap is inappropriate.

For univoltine (one generation per year) insects like the bay checkerspot or annual plants, a *discrete time* model, with popu-

Think of other species for which the continuous model is inappropriate.

Which model do you think would be best for humans?

Box 2.2. Solution for exponential growth in discrete time.

The solution to

$$N_{t+1} = RN_t$$

is

$$N_t = R^t N_0.$$

This equation and its solution will be used many times as well. The *qualitative* behavior of the solution is determined only by the difference between R and 1.

- For $R > 1$, the solution increases without bound
- for $R = 1$, the solution is a constant
- for $R < 1$, the solution approaches 0.

We will see the contrast between discrete time and continuous time arising throughout the book. We would expect that in most cases the conclusions we draw should not depend on this difference. However, in several cases the difference between discrete time and continuous time is critical.

lation measurements only taken at fixed times, is more appropriate. We will measure time in units of generations, which may be 1 year. Here we will let R be the number of individuals in the next generation per individual in the current generation. Thus, if N_t is the number of individuals in the population at generation t,

$$N_{t+1} = RN_t. \tag{2.10}$$

From the relationship

$$N_2 = RN_1 = R(RN_0) = R^2 N_0 \tag{2.11}$$

Use $N_1 = RN_0$ in equation (2.11).

we conclude that

$$N_t = R^t N_0. \tag{2.12}$$

After 2 years there is a 2 in the exponent so we expect that after t years there will be a t in the exponent.

Thus, once again, we see that growth is exponential or geometric. The qualitative behavior of the solution is illustrated in Figure 2.2 and discussed in Box 2.2. Note that we reach the same biological and mathematical conclusions from this model that we reached using the continuous time model.

Relationship between continuous and discrete models

We have two models differing only in the assumption of discrete versus overlapping generations. What is the connection between these two models? Comparing the solutions of the two models given in equations (2.9) and (2.12), we see that R^t and $e^{rt} = (e^r)^t$ play analogous roles. Thus we conclude that

$$R = e^r \qquad (2.13)$$

or

$$\ln(R) = r. \qquad (2.14)$$

If r is small, or analogously if R is close to 1, we can use Taylor series to find the approximate relationship:

$$R \approx 1 + r. \qquad (2.15)$$

The Taylor series for e^r is
$$e^r \approx 1 + r + \frac{r^2}{2} + \cdots.$$

Can you think of a heuristic explanation why this equation has a 1 in it and is not simply $R \approx r$?

We conclude that both the continuous time and discrete time models make similar predictions. As we consider more realistic situations we will extend both these models, often choosing which one to use on the basis of mathematical convenience as well as for biological reasons.

In continuous time, $r = 0$ corresponds to a population that remains the same size, while in discrete time $R = 1$ corresponds to a population that remains the same size.

Exponential growth in nature

We have seen in Figures 2.1 and 2.2 some hypothetical examples of population growth. What are typical values of per capita growth rates in laboratory and natural populations? In the laboratory, estimates of r or R can show quite rapid population growth, but in natural populations r is almost always near zero and R near one. As we have noted, a population that does not show such values of growth will either explode in numbers or disappear rapidly.

One example of exponential growth in nature is illustrated in Figure 2.3. Here the collared dove numbers initially grew approximately exponentially, but after some years, the growth was no longer exponential. In Chapter 4, we will try to understand this aspect of population dynamics.
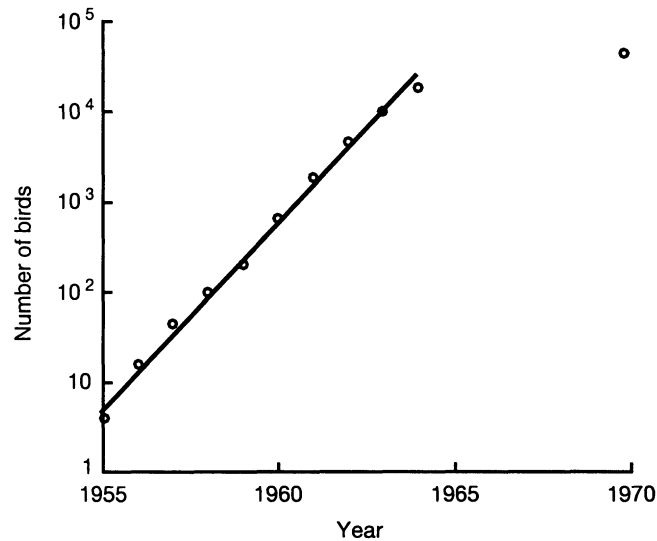
FIGURE 2.3. Dynamics of population growth for collared dove in Great Britain. Note the log scale, so the straight line fit through the population counts implies the growth is approximately exponential until about 1963 (data from Hudson, 1965, 1972). The last data point (1970), which is far below the level that would be reached if exponential growth continued, is an estimate because the population had become too large to count accurately.

The fundamental question of population ecology

What can we conclude about the simple models that we have just considered? As noted, the prediction of exponential growth can be valid only for a short period of time. Thus the assumptions of the models, in particular the assumption that the rate of population growth is proportional to the number of individuals (the assumption of *density independence*), must be in error. The fundamental question of population biology is to determine the causes and consequences of the deviation from exponential growth, or simply what regulates populations.

Population sizes reach absurdly high levels if exponential growth continues for more than a short time. Here, we admit some circularity – we are calling a time short if it is short enough that exponential growth makes sense. Problem 1 helps make this idea more concrete.

2.2   Age structure: the simplest case

Before we examine the consequences of density dependence, we continue our study of density independence by looking at models

more appropriate for organisms that reproduce many times, still assuming density-independent birth and death rates.

Many species of interest to ecologists do not have the simple life history that allows us to blindly use the models we have just developed. The common snapping turtle (*Chelydra serpentina*) has a life history typical of many other turtles (Congdon et al., 1994). Females do not become sexually mature until they are more than 5 years old, and continue to lay eggs essentially throughout their life, which may be as long as 100 years. How should we understand the dynamics of this species? The models we have developed do not seem to apply. Understanding the dynamics of long-lived species is important for many conservation questions, as many long-lived species are endangered.

A life history is the pattern of births and deaths (and possibly dispersal patterns) for a population.

Many mammals also are not well described by the simple models we have just developed. Humans, for example, have different fecundities as a function of age, as do virtually all but the simplest animals or plants. If, in addition, generations overlap so that different ages are present at the same time, we need to modify our models because we have thus far assumed that generations do not overlap.

In general, mammals do exhibit one characteristic that allows us to simplify our models. We will focus on females, looking only at the reproduction of females and only at female births. This assumption is justified if males are not limiting reproduction in the species.

Can you think of populations where the simplification of considering only females would be wrong? Why?

A very simple model

Before considering forces that prevent populations from growing exponentially, we will consider whether our prediction of exponential growth holds in a slightly more complex setting where we include age structure. Rather than start with a general model, we will study a hypothetical organism that lives for 2 years, potentially reproducing either at age 1 or at age 2.

Most biennial plants, plants that reproduce after 2 years, are unable to reproduce after 1 year.

We assume, as earlier, that the per capita birth rate and the survival rate are unaffected by the number of individuals present. However, birth rates and death rates will depend on the ages of the individuals. Count individuals at the end of any season, and

The approach we take, of looking at an idealized – perhaps unrealistically simplified – case that does however capture the essence of a biological interaction, is a very important approach for elucidating general principles.
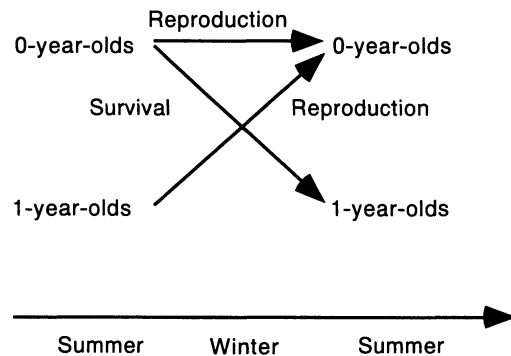
FIGURE 2.4. Life history of a population with two age classes

There is nothing special about 83 and 82; we are choosing two years to use as examples.

determine the growth rate. For example, look at the end of the 83rd season to get $R = N_{83}/N_{82}$. Without age structure, we would have exponential growth with $N_{84} = RN_{83}$. Does this relationship hold even with age structure?

In answering this question we make a fundamental assumption by considering only females and only female births in populations with two sexes, as we noted. Next, we need to set up the parameters in a model to answer this question. We will call an organism 0 years old during its first year of life and 1 year old during its second year. We will assume that all individuals die before they reach their third year. The parameters and variables we need to describe this are as follow:

- m_0 is the mean number of offspring of a 0-year-old the following year.

- m_1 is the mean number of offspring of a 1-year-old the following year.

- S_0 is the probability that a 0-year-old survives to become a 1-year-old.

- $n_0(t)$ is the number of 0-year-olds at time t.

- $n_1(t)$ is the number of 1-year-olds at time t.

- $N(t) = n_0(t)+n_1(t)$ is the total number of organisms at time t.

We first describe the model in words, and then in equations.

$n_0(t + 1)$ = number of offspring of 0-year-olds in year t
                  + number of offspring of 1-year-olds in year t

$n_1(t + 1)$ = number of 0-year-olds in year t times
            the probability of survival from 0 to 1

Translating this into equations, we find that

$$n_0(t + 1) = n_0(t)m_0 + n_1(t)m_1 \qquad (2.16)$$

$$n_1(t + 1) = n_0(t)S_0. \qquad (2.17)$$

We are now prepared to answer the question we just posed: does a population grow exponentially even if age structure in reproduction is important? We can rephrase this question as: is there a unique growth rate for the population that is not dependent on how much time has elapsed since the population was established? What happens if in year 0 we have 10 zero-year-olds and no one-year-olds, so that $n_0(0) = 10$ and $n_1(0) = 0$ are the starting sizes in each age class? Using equations (2.16) and (2.17), we see that next year

$$n_0(1) = 10m_0 \qquad (2.18)$$

$$n_1(1) = 10S_0. \qquad (2.19)$$

On the other hand, if in year 0 we have no zero-year-olds and 10 one-year-olds, so that $n_0(0) = 0$ and $n_1(0) = 10$, using (2.16) and (2.17), we see that next year

$$n_0(1) = 10m_1 \qquad (2.20)$$

$$n_1(1) = 0. \qquad (2.21)$$

These are very different populations (unless of course we choose special values for the parameters), so we conclude that no single number represents a growth rate.

How could we get a specific, constant growth rate? Every 0-year-old always makes the same contribution to the population the next year, but the contribution of 1-year-olds is different from that of 0-year-olds. If the ratio of 0-year-olds to 1-year-olds stays the same, then we expect that the growth rate of the population stays the same.

Are there conditions where the ratio of 0-year-olds to 1-year-olds remains the same? Let us assume that there are and see what happens. We will see later that the assumption that the growth

For example, let $m_0=1$, $S_0 = \frac{1}{2}$, and $m_1 = 2$. Then, starting with all zero-year-olds, we have 10 zero-year-olds and 5 one-year-olds in the first year. However, starting with all one-year-olds, we have 20 zero-year-olds and no one-year-olds in the first year.

rate stays the same implies that the ratio of 0-year-olds to 1-year-olds stays the same and vice versa. First let us assume that $n_1(t) = cn_0(t)$, where c is the ratio of one-year-olds to zero-year-olds. Then, substituting into the model (2.16) and (2.17), we find

To get these equations, we replace $n_1(t)$ everywhere it appears in (2.16) by $cn_0(t)$.

$$n_0(t + 1) = n_0(t)m_0 + cn_0(t)m_1 \qquad (2.22)$$

$$cn_0(t + 1) = n_0(t)S_0. \qquad (2.23)$$

In (2.22) and (2.23), we view the ratio c as the unknown.

We now try to find a ratio c that is constant from generation to generation, by eliminating $n_0(t + 1)$ and $n_0(t)$ from equations (2.22) and (2.23). From (2.23) we find

$$n_0(t + 1) = n_0(t)S_0/c. \qquad (2.24)$$

Substituting this expression into (2.22) we get

$$n_0(t)S_0/c = n_0(t)m_0 + cn_0(t)m_1. \qquad (2.25)$$

Dividing by $n_0(t)$ yields a quadratic equation for c, which we can solve using the quadratic formula:

$$S_0/c = m_0 + cm_1 \qquad (2.26)$$

$$S_0 = m_0c + c^2m_1 \qquad (2.27)$$

$$0 = m_1c^2 + m_0c - S_0 \qquad (2.28)$$

$$c = \frac{-m_0 \pm \sqrt{m_0^2 + 4S_0m_1}}{2m_1} \qquad (2.29)$$

Thus there are two possible solutions c for a ratio of 0-year-olds to 1-year-olds that remains constant from year to year. If the sign is + in (2.29), the ratio c is positive, while if the sign is − the ratio is negative. From (2.24) we see that the growth rate of the population is S_0/c, so for the positive value of c, S_0/c is a candidate for the growth rate of the population. We will return to the meaning of the negative possibility.

The growth rate is $n_0(t + 1)/n_0(t)$.

What happens if the population does not start off at the 'magic' ratio of 0-year-olds to 1-year-olds? As we will see below, through time the population will approach both the ratio of 0-year-olds and 1-year-olds and the growth rate we have just found.

Box 2.3. Matrices and vectors.

We will find matrices and vectors useful for expressing many of the models we study, as a compact notation for expressing linear equations.

- A *matrix* is a rectangular array of numbers, for example

$$\begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix}.$$

This is a 2 × 2 matrix, where the first 2 refers to the number of rows and the second 2 refers to the number of columns.

- A column *vector* is a matrix with only 1 column

$$\begin{pmatrix} u_1 \\ u_2 \end{pmatrix}.$$

- A row vector is a matrix with only one row.

$$\begin{pmatrix} u_1 & u_2 \end{pmatrix}.$$

When we say vector in this text we almost always mean column vector.

Using matrices to write the model

A much more convenient notation, essential for extending the model to include more age classes, is to use *matrices*. If you are unfamiliar with matrix notation and matrix multiplication, these concepts are described in Boxes 2.3 through 2.7. We can write the model (2.16) and (2.17) using matrices as

$$\begin{pmatrix} m_0 & m_1 \\ S_0 & 0 \end{pmatrix} \begin{pmatrix} n_0(t) \\ n_1(t) \end{pmatrix} = \begin{pmatrix} n_0(t+1) \\ n_1(t+1) \end{pmatrix}. \tag{2.30}$$

As we have just done, we will assume that the ratio of 0-year-olds to 1-year-olds remains constant and the population grows at the rate λ per year. (In the previous section, the growth rate was S_0/c.) We call this ratio of individuals at different ages that remains constant a *stable age distribution*. As we will see, not only does the ratio of the numbers of individuals at different ages remain

We will see the concept of stability throughout this book.

Box 2.4. Matrix addition and subtraction.

The general rule for adding or subtracting matrices of vectors is that corresponding elements are added or subtracted. Thus,

$$\begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix} + \begin{pmatrix} b_{11} & b_{12} \\ b_{21} & b_{22} \end{pmatrix} = \begin{pmatrix} a_{11} + b_{11} & a_{12} + b_{12} \\ a_{21} + b_{21} & a_{22} + b_{22} \end{pmatrix}.$$

As an example:

$$\begin{pmatrix} 2 & 3 \\ 4 & 5 \end{pmatrix} - \begin{pmatrix} 1 & 2 \\ 3 & 1 \end{pmatrix} = \begin{pmatrix} 1 & 1 \\ 1 & 4 \end{pmatrix}.$$

Box 2.5. Matrix multiplication.

The general formula for multiplying a matrix times a vector is:

$$\begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix} \begin{pmatrix} u_1 \\ u_2 \end{pmatrix} = \begin{pmatrix} a_{11}u_1 + a_{12}u_2 \\ a_{21}u_1 + a_{22}u_2 \end{pmatrix}$$

As an example:

$$\begin{pmatrix} 2 & 3 \\ 4 & 5 \end{pmatrix} \begin{pmatrix} 6 \\ 7 \end{pmatrix} = \begin{pmatrix} (2 \cdot 6) + (3 \cdot 7) \\ (4 \cdot 6) + (5 \cdot 7) \end{pmatrix} = \begin{pmatrix} 33 \\ 59 \end{pmatrix}.$$

---

constant at the stable age distribution, but *the stable age distribution is approached from other age distributions*. This is why we use the word stable, to emphasize that this age distribution is approached. The notion of a stable age distribution is central to the understanding of the dynamics of age-structured populations.

One fact about the stable age distribution is important to emphasize here. The stable age distribution refers to the ratios of the numbers of individuals at different ages and not to the absolute numbers. Thus, the stable age distribution is not unique – if 10 zero-year-olds and 5 one-year-olds is a stable age distribution, so is 20 zero-year-olds and 10 one-year-olds.

Box 2.6. Multiplying a matrix by a scalar.

A scalar is just a single number. To multiply a matrix by a scalar, simply multiply each element in the matrix by the scalar.

$$\lambda \begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix} = \begin{pmatrix} \lambda a_{11} & \lambda a_{12} \\ \lambda a_{21} & \lambda a_{22} \end{pmatrix}.$$

As an example:

$$4 \begin{pmatrix} 2 & 3 \\ 4 & 5 \end{pmatrix} = \begin{pmatrix} 8 & 12 \\ 16 & 20 \end{pmatrix}$$

We now express the assumption that the population is in a stable age distribution in matrix and vector notation. The idea is that in every year the ratio of 0-year-olds to 1-year-olds remains constant, but that the number in each age class grows at the rate λ each year. In vector and matrix notation, we write

$$\begin{pmatrix} m_0 & m_1 \\ S_0 & 0 \end{pmatrix} \begin{pmatrix} n_0 \\ n_1 \end{pmatrix} = \begin{pmatrix} \lambda n_0 \\ \lambda n_1 \end{pmatrix}. \tag{2.31}$$

There is no t in (2.31) because we assume that the stable age equation holds year after year.

In honor of P.H. Leslie, who was one of the first to describe the use of matrices to describe population dynamics with age structure in papers published in 1945 and 1948, we will call the matrix in this equation a *Leslie matrix* and denote it by L. We will let N be the vector of population sizes, so

$$N = \begin{pmatrix} n_0 \\ n_1 \end{pmatrix} \tag{2.32}$$

We can then write our equation for the stable age distribution in the even more compact form

$$LN = \lambda N \tag{2.33}$$

What is noteworthy about this expression is that it is valid for an arbitrary number of age classes. We wish to determine a formula for λ from this expression, but we cannot simply divide by the vector N. Beginning with (2.33) we write

Based on our example in the previous section we expect two possible solutions for λ.

Box 2.7. The identity matrix.

If we multiply any number by 1 the answer is just the number we started with. The number 1 is called the (multiplicative) identity. The matrix that plays the same role is called the identity matrix and is denoted by I, so $IN = N$ for any matrix or vector N of the appropriate size. The identity matrix with two rows and columns is

$$I = \begin{pmatrix} 1 & 0 \\ 0 & 1 \end{pmatrix}.$$

Try it and see.

$$LN - \lambda N = 0 \tag{2.34}$$

$$LN - \lambda IN = 0 \tag{2.35}$$

$$(L - \lambda I)N = 0 \tag{2.36}$$

where I is the identity matrix, as explained in Box 2.7. A fact from matrix algebra is that the final equation is satisfied (for nonzero N) if and only if the *determinant* of $(L - \lambda I)$ is 0. We will use this fact without trying to justify it. The formula for the determinant of a 2 × 2 matrix is

We want N to be nonzero as this is a vector of population sizes.

$$\det \begin{pmatrix} a_{11} - \lambda & a_{12} \\ a_{21} & a_{22} - \lambda \end{pmatrix} = (a_{11} - \lambda)(a_{22} - \lambda) - a_{12}a_{21}. \tag{2.37}$$

Setting this determinant to be 0 yields a quadratic equation for the growth rate λ.

We will work through an example. Let $m_0 = 1$, $m_1 = 4$, and $S_0 = 1/2$. Then,

$$L = \begin{pmatrix} 1 & 4 \\ 1/2 & 0 \end{pmatrix} \tag{2.38}$$

and

$$L - \lambda I = \begin{pmatrix} 1 - \lambda & 4 \\ 1/2 & -\lambda \end{pmatrix}. \tag{2.39}$$

Here the equation satisfied by λ, (2.41), can be factored, but in general we have to use the quadratic formula.

Setting the determinant of $L - \lambda I$ equal to 0 yields

$$(1 - \lambda)(-\lambda) - 2 = 0 \tag{2.40}$$

$$\lambda^2 - \lambda - 2 = 0 \qquad\qquad (2.41)$$

$$(\lambda - 2)(\lambda + 1) = 0, \qquad\qquad (2.42)$$

so the two solutions are $\lambda = 2$ or $\lambda = -1$. We will substitute each growth rate in turn into (2.33), with L given by (2.38), to find the stable age distribution we defined earlier and to understand what the second 'growth rate' really means. With $\lambda = 2$, we find that (2.33) is

$$\begin{pmatrix} 1 & 4 \\ 1/2 & 0 \end{pmatrix} \begin{pmatrix} n_0 \\ n_1 \end{pmatrix} = \begin{pmatrix} 2n_0 \\ 2n_1 \end{pmatrix} \qquad\qquad (2.43)$$

Both the linear equations expressed by this single matrix equation are satisfied if $n_0 = 4n_1$, which is the stable age distribution. Thus if there are four times as many 0-year-olds as there are 1-year-olds, the population will double each year.

The first equation is $n_0 + 4n_1 = 2n_0$ which simplifies to $n_0 = 4n_1$.

If we choose $\lambda = -1$, we find that (2.33), with L given by (2.38), is

$$\begin{pmatrix} 1 & 4 \\ 1/2 & 0 \end{pmatrix} \begin{pmatrix} n_0 \\ n_1 \end{pmatrix} = \begin{pmatrix} -n_0 \\ -n_1 \end{pmatrix} \qquad\qquad (2.44)$$

Both the linear equations expressed by this single matrix equation are satisfied if $n_0/2 = -n_1$. Does this second 'growth rate' have any biological meaning? A numerical example will help answer this question.

What happens if the population starts with 6 zero-year-olds and no one-year-olds? We compute the dynamics as follows:

We write our starting vector of population size as the sum of the two vectors we just found.

$$\begin{pmatrix} 1 & 4 \\ 1/2 & 0 \end{pmatrix} \begin{pmatrix} 4+2 \\ 1+(-1) \end{pmatrix} = \begin{pmatrix} 8+(-2) \\ 2+1 \end{pmatrix} = \begin{pmatrix} 6 \\ 3 \end{pmatrix} \qquad (2.45)$$

$$\begin{pmatrix} 1 & 4 \\ 1/2 & 0 \end{pmatrix} \begin{pmatrix} 8+(-2) \\ 2+1 \end{pmatrix} = \begin{pmatrix} 16+2 \\ 4+(-1) \end{pmatrix} = \begin{pmatrix} 18 \\ 3 \end{pmatrix} \qquad (2.46)$$

$$\begin{pmatrix} 1 & 4 \\ 1/2 & 0 \end{pmatrix} \begin{pmatrix} 16+2 \\ 4+(-1) \end{pmatrix} = \begin{pmatrix} 32+(-2) \\ 8+1 \end{pmatrix} = \begin{pmatrix} 30 \\ 9 \end{pmatrix} \qquad (2.47)$$

Do you notice a pattern? From the first time step we can 'break up' the numbers in the population into two components, one corresponding to the stable age distribution, and the other corresponding to a deviation from the stable age distribution. With increasing time, the deviation from the stable age distribution rep-

year	0-year-olds	1-year-olds	total	growth rate	ratio
0	6	0	6		
1	6	3	9	1.500	2.000
2	18	3	21	2.333	6.000
3	30	9	39	1.857	3.333
4	66	15	81	2.077	4.400
5	126	33	159	1.963	3.818
6	258	63	321	2.019	4.095
7	510	129	639	1.991	3.953
8	1026	255	1281	2.005	4.024
9	2046	513	2559	1.998	3.988
10	4098	1023	5121	2.001	4.006
11	8190	2049	10239	1.999	3.997
12	16386	4095	20481	2.000	4.001

TABLE 2.1. Dynamics with age structure: a numerical example.

resents a smaller and smaller fraction of the total population. *We have shown that the stable age distribution is indeed stable – it is approached from other age distributions.* Because the stable age distribution is approached through time, an observation of a population that is not in a stable age distribution is evidence that the population has been disturbed at some time.

Can we write down, in a simple form, what the population will be after t years? As in the model without age structure, we start with the change in population over 1 year, $N_1 = LN_0$, and deduce the long-term description,

This is the analog to equation (2.11).

$$N_t = L^t N_0, \qquad (2.48)$$

where L^t means to multiply by the Leslie matrix t times. To understand the long-term dynamics, we need a simple expression for $L^t N_0$.

Eigenvalues will also play an essential role in our study of interactions between two species.

We can express the population after an arbitrary number of years, $L^t N_0$, in a simple form using *eigenvectors* and *eigenvalues* (defined in Boxes 2.8 and 2.9). Let λ_0 and λ_1 be the two eigenvalues and v_0 and v_1 be the two corresponding eigenvectors. Our first step is to express the initial population size as the sum of the

two eigenvectors, so

$$N_0 = a_0 v_0 + a_1 v_1, \qquad (2.49)$$

where the constants a_0 and a_1 can be determined from solving linear equations.

Using this expression for the initial population, we can find the population after t years as

$$N_t = L^t N_0 = L^t(a_0 v_0 + a_1 v_1) \qquad (2.50)$$

$$= a_0 L^t v_0 + a_1 L^t v_1 \qquad (2.51)$$

$$= a_0 \lambda_0^t v_0 + a_1 \lambda_1^t v_1. \qquad (2.52)$$

To go from (2.50) to (2.51) use the distributive law, and remember that a_0 is a scalar (a single number), so we can move it to the left of L^t.

To go from (2.51) to (2.52), remember that $L v_0 = \lambda_0 v_0$. Do this t times for each eigenvector.

From equation (2.52), we can read off the important property of populations approaching the stable age distribution. Assume that we have labeled the eigenvalues so that $|\lambda_0| > |\lambda_1|$; then λ_0 is what we have been calling the *growth rate* of the population. After a long time, as t becomes large, the term $a_0 \lambda_0^t v_0$ in (2.52), the expression for the population size after an arbitrary number of years, will be much larger than the term $a_1 \lambda_1^t v_1$. In fact, ignoring the smaller term, we will have $N_t \approx a_0 \lambda_0^t v_0$, so the population will be in the stable age distribution.

What role will the relative sizes of the eigenvalues play in the rate of approach to the stable age distribution? The answer again lies in (2.52).

In this chapter, we have focused for simplicity on two age classes. For an arbitrary number of age classes, our conclusions about the approach to a stable age distribution still hold so long as each age class has a possibility of a descendant in any given year far enough in the future.

Iteroparity versus semelparity

An organism that reproduces just once during its lifetime is called *semelparous*, while an organism that reproduces many times is called *iteroparous*. Examples of semelparous organisms are salmon and periodical cicadas. Oak trees, humans, and turtles are examples of iteroparous species. For organisms that live only 2 years, what would the Leslie matrix of a semelparous organism look like? There would be a zero in the upper left hand corner:

$$\begin{pmatrix} 0 & m_1 \\ S_0 & 0 \end{pmatrix} \qquad (2.53)$$

Box 2.8. Eigenvalues of a 2 × 2 matrix.

We will refer to the formula for the eigenvalues (growth rates) many times. For the 2 × 2 matrix

$$\begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix}$$

the two eigenvalues λ are the two solutions of the quadratic equation

$$0 = (a_{11} - \lambda)(a_{22} - \lambda) - a_{12}a_{21}$$

$$= \lambda^2 - (a_{11} + a_{22})\lambda + (a_{11}a_{22} - a_{12}a_{21}).$$

The two eigenvalues can be found by solving this equation using the quadratic formula.

Note that in this case the number of 0-year-olds in year 1 has no effect on the number of 0-year-olds in year 2; there really are two separate populations corresponding to the two year classes. In this case, there is no approach to the stable age distribution. Populations of species that come close to this idealized situation of reproducing only once at a fixed age approach the stable age distribution very slowly.

Data

How do we obtain the data used to estimate population growth rates using the model we have just developed? We will consider the more general case where there is an arbitrary number of age classes, noting only that the length of each age class must be the same. We call the description of age-specific birth and death rates the *life table*. The quantities that we will use in the life table are as follow:

Why is $l_0 = 1$?

- l_x is the fraction of newborn individuals that survive to age x.

What is the relationship among l_x, l_{x+1}, S_x?

- S_x is the probability of surviving from age x to age $x + 1$.

- m_x is the average birth rate for an individual of age x.

Box 2.9. Eigenvectors of a 2 × 2 matrix.

We will need to use the formula for eigenvectors many times. For the 2 × 2 matrix

$$L = \begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix}$$

there are two eigenvalues, λ_0 and λ_1. To find the eigenvector v_0 corresponding to the eigenvalue λ_0 that satisfies $Lv_0 = \lambda_0 v_0$ first try a vector of the form

$$\begin{pmatrix} 1 \\ b \end{pmatrix}$$

which leads to the equations

$$a_{11} + a_{12}b = \lambda_0$$
$$a_{21} + a_{22}b = \lambda_0 b$$

for b. In general each equation will have the same solution for b. If these equations do not have a solution for b, try a vector of the form

$$\begin{pmatrix} b \\ 1 \end{pmatrix},$$

which leads instead to the equations

$$a_{11}b + a_{12} = \lambda_0 b$$
$$a_{21}b + a_{22} = \lambda_0$$

for b.
The second eigenvector is found in a similar fashion.

There are two different approaches for obtaining the data in a life table, with different advantages and disadvantages.

Vertical life tables

For organisms that live only a short time (less than the length of time spent collecting the data), one can determine the schedule of age-dependent per capita birth and death rates by following a sin-

Box 2.10. Finding the stable age distribution and growth rate of a population with two age classes.

We will give an example of the whole procedure. Let the birth rate of 0-year-olds be 2, the birth rate of 1-year-olds 4, and the survival rate 1/4. Then the Leslie matrix is

$$\begin{pmatrix} 2 & 4 \\ 1/4 & 0 \end{pmatrix}.$$

The two growth rates are the solutions of the quadratic equation

$$\lambda^2 - 2\lambda - 1 = 0.$$

Using the quadratic formula we find the solutions

$$\lambda_0, \lambda_1 = \frac{2 \pm \sqrt{8}}{2}.$$

Thus, the larger value of λ corresponding to the growth rate is 2.414. If we look for a stable age distribution of the form $Lv_0 = \lambda_0 v_0$, we first try a vector of the form

$$\begin{pmatrix} 1 \\ b \end{pmatrix}.$$

We find that b satisfies

$$2 + 4b = 2.414$$

so a stable age distribution is

$$\begin{pmatrix} 1 \\ 0.1035 \end{pmatrix}.$$

Remember that the stable age distribution is not unique, so that

$$\begin{pmatrix} 4 \\ 0.414 \end{pmatrix}$$

is also a stable age distribution.

TABLE 2.2. Life table for the vole *Microtus agrestis* reared in the laboratory (data from Leslie and Ranson 1940).

age (weeks)	x	l_x	m_x
0	0	1.0000	0.0000
8	1	0.8335	0.6504
16	2	0.7313	2.3939
24	3	0.5881	2.9727
32	4	0.4334	2.4662
40	5	0.2928	1.7043
48	6	0.1813	1.0815
56	7	0.1029	0.6683
64	8	0.0535	0.4286
72	9	0.0255	0.3000

gle *cohort* through time. Start with a fixed number of organisms, and record births and deaths through time. A major disadvantage of this method is the requirement that the maximum age of the organism investigated must be short enough. One example of data of this kind is in Table 2.2. Many more examples are included in Andrewartha and Birch (1954). This is called a *vertical life table* because we think of time as running down the page on which the observations are written.

A cohort is all the individuals born at a single time.

Horizontal life tables

For very long-lived organisms, such as elephants, turtles, and most trees, following a single cohort through time is impractical. Instead, one collects data from a single point in time and estimates birth rates and death rates. This method has several disadvantges because of the implicit assumptions made. In particular, as we will soon see, the ratio of 5-year-olds to 4-year-olds in the current population is usually not the probability of survival from 4 to 5 years. There also needs to be a way of accurately estimating the age of organisms.

This way of getting the life history parameters is called a *horizontal life table*, because the observations are made at a single time. In fact, this approach usually involves estimating some of

TABLE 2.3. Life table for the snapping turtle (Congdon et al., 1994). For $x > 14$, $l_x = 0.93 l_{x-1}$, which is an estimate.

age in years (x)	S_x	l_x	m_x
0	0.230	1.00000	0.0
1	0.470	0.23000	0.0
2	0.810	0.10810	0.0
3	0.650	0.08756	0.0
4	0.650	0.05691	0.0
5	0.750	0.03699	0.0
6	0.740	0.02775	0.0
7	0.810	0.02053	0.0
8	0.770	0.01663	0.0
9	0.800	0.01281	0.0
10	0.820	0.01024	0.0
11	0.820	0.00840	4.0
12	0.820	0.00689	6.0
13	0.930	0.00565	8.0
14	0.930	0.00525	10.0
15 – 105	0.930		12.0

the life table parameters. This is illustrated by the example given in Table 2.3.

With detailed data on age-dependent births and deaths such as those for the snapping turtle or vole, one could construct a large Leslie matrix. However, this is an unwieldy approach. There is an alternative approach that is easier to apply in practice. We will first phrase the approach as a *continuous time model*, and then explain how to use data collected in discrete time, such as the life table data we have just seen, in the model.

Continuous time model

Many species, such as humans and some insects, are best described by a continuous time model of age-structured growth. We will use our experience with the discrete time model to derive the continuous time model. As we will see this model is the basis of many estimates for the *intrinsic rate of increase*, as in Andrewartha and Birch (1954).

We use the following quantities to formulate the model:

- $B(t)$ is the total birth rate in the population.

- $l(x)$ is the fraction of newborn individuals that survive to age x.

- $m(x)$ is the average birth rate for an individual of age x.

To find the total birth rate we sum the births to individuals of all possible ages. This leads to

Recall from your calculus class that integrals are really just sums.

$$B(t) = \int_0^\infty \left(\text{rate of births to parents of age } x\right) dx. \qquad (2.54)$$

We now determine the birth rate in equation (2.54), using the following reasoning:

- Rate of births to parents of age x = $m(x)$ times number of individuals of age x.

- Number of individuals of age x = number of births x years ago times fraction of newborn who survive to age x.

- Number of individuals of age x = $B(t - x)l(x)$.

We substitute into equation (2.54) to obtain a single equation relating the birth rate now to the birth rates in the past:

We call this a renewal equation, because it describes how the population is renewed through births.

$$B(t) = \int_0^\infty B(t - x)l(x)m(x)dx. \qquad (2.55)$$

We solve this equation under the assumption that the population is in a stable age distribution. Thus, we assume that growth is exponential at the rate r, where we again use the symbol r to represent the intrinsic rate of increase of the population. This can be expressed as

From our analysis of the Leslie matrix formulation, we expect that there will be a stable age distribution.

$$B(t) = e^{rt}B(0). \qquad (2.56)$$

Because equation (2.55) also depends on the birth rate at time $t - x$, we rewrite equation (2.56) as:

$$B(t - x) = e^{r(t-x)}B(0). \qquad (2.57)$$

Now, substitute these last two relations into the renewal equation (2.55) to obtain

$$e^{rt}B(0) = \int_0^\infty e^{r(t-x)}B(0)l(x)m(x)dx. \qquad (2.58)$$

$e^{r(t-x)}/e^{rt} = e^{-rx}$

Now divide both sides by $e^{rt}B(0)$ to arrive at *Euler's equation*:

$$1 = \int_0^\infty e^{-rx} l(x)m(x)dx. \qquad (2.59)$$

Note that this equation can be used to find r if we know the life table for a particular organism. However, the birth rates and survival probabilities cannot be measured over continuous time, only at discrete intervals. When this equation is used to estimate r, ecologists usually use a discrete approximation obtained by replacing the integral with a sum

Remember that $\sum_{x=0}^{\infty} e^{-rx} l_x m_x$ means $e^{-0r} l_0 m_0 + e^{-1r} l_1 m_1 + e^{-2r} l_2 m_2 + \ldots$

$$1 = \sum_{x=0}^{\infty} e^{-rx} l_x m_x. \qquad (2.60)$$

We have also used the notation l_x and m_x to emphasize that these quantities are defined only at discrete ages. An estimate for r can be found from this equation numerically, as the right-hand side of the equation is monotonic decreasing in r: as r increases the sum always decreases.

We demonstrate this using the data from the vole. By plotting the quantity $\sum_{x=0}^{\infty} e^{-rx} l_x m_x$ against r, we can find the value of r that makes the sum 1. Using this reasoning as shown in Figure 2.5, and then improving the estimate by trying different values of r, we find that the rate of increase for the vole population is approximately 0.7 per 8 weeks.

There is another quantity that is often calculated from the life table, the *net reproduction rate* R_0, which is average total number of (female) offspring produced by a single (female) individual in her lifetime. Try to describe in words why this is given by

$$R_0 = \int_0^\infty l(x)m(x)dx. \qquad (2.61)$$

Can you have $r > 0$ and $R_0 < 1$?

What is the relationship between R_0 and r? For the vole population, we find R_0 is 5.90.

Stable age distribution

It is easy to determine the stable age distribution using the framework we have developed here. Denote by $c(x)$ a *density function* for the fraction of individuals of age x in the stable age distribu-
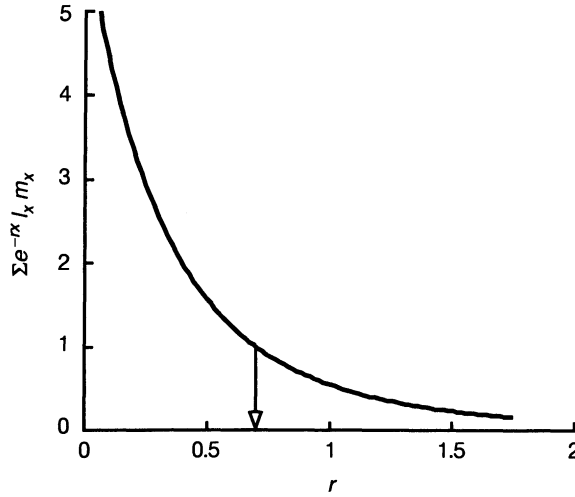
FIGURE 2.5. Plot of $\sum_{x=0}^{8} e^{-rx} l_x m_x$ against different values of r for the vole population whose life table is given in Table 2.2. We find the actual growth rate for this population by finding the value of r that makes the sum 1. As indicated by the arrow on the figure this value is approximately $r = 0.7$.

tion. This means that the fraction of individuals between ages x and $x + dx$ is given by $\int_x^{x+dx} c(z)dz \approx c(x)dx$. Thus, in words

$$c(x) = \frac{\text{number of individuals of age } x}{\text{total number of individuals}}. \qquad (2.62)$$

To find a mathematical formula that expresses this descriptive quotient, first note that the total number of individuals is given by

$$\int_0^{\infty} \left(\text{number of individuals of age } x\right) dx. \qquad (2.63)$$

One expression for the number of individuals (actually a density function) results from observing that an individual is 10 years old today if it was born 10 years ago and has survived. Thus the number of individuals of age x is given by $B(t - x)l(x)$. Try to determine the reasoning embodied in the following sets of equations:

$$c(x) = \frac{B(t - x)l(x)}{\int_0^{\infty} B(t - z)l(z)dz} \qquad (2.64)$$

At the stable age distribution, $B(t - x) = e^{r(t-x)}B(0)$. To go from (2.65) to (2.66), divide numerator and denominator by e^{rt}.

TABLE 2.4. Life table and demographic functions for the vole *Microtus agrestis* reared in the laboratory (data from Leslie and Ranson 1940).

age (weeks)	x	l_x	m_x	$l_x m_x$	$e^{-rx}l_x$	c_x	$e^{-rx}l_x m_x$	v_x/v_0
0	0	1.0000	0.0000	0.0000	1.0000	0.5862	0.0000	1.0000
8	1	0.8335	0.6504	0.5421	0.4142	0.2428	0.2694	2.4145
16	2	0.7313	2.3939	1.7507	0.1806	0.1059	0.4323	4.0461
24	3	0.5881	2.9727	1.7482	0.0722	0.0423	0.2145	4.1348
32	4	0.4334	2.4662	1.0689	0.0264	0.0155	0.0652	3.1731
40	5	0.2928	1.7043	0.4990	0.0089	0.0052	0.0151	2.1062
48	6	0.1813	1.0815	0.1960	0.0027	0.0016	0.0030	1.3063
56	7	0.1029	0.6683	0.0687	0.0008	0.0005	0.0005	0.7974
64	8	0.0535	0.4286	0.0229	0.0002	0.0001	0.0001	0.4997
72	9	0.0255	0.3000	0.0076	0.0000	0.0000	0.0000	0.3000

$$= \frac{e^{r(t-x)}B(0)l(x)}{\int_0^\infty e^{r(t-z)}B(0)l(z)dz} \tag{2.65}$$

$$= \frac{e^{-rx}l(x)}{\int_0^\infty e^{-rz}l(z)dz} \tag{2.66}$$

To go from (2.66) to (2.67), approximate the integral by a sum.

$$\approx \frac{e^{-rx}l_x}{\sum_{x=0}^\infty e^{-rx}l_x} \tag{2.67}$$

We can thus find an approximation for the stable age distribution from life table data. The presence of the factor e^{-rx} in (2.67) means that the stable age distribution depends not only on the survivorship rates but also on the intrinsic rate of increase. Equation (2.67) gives the stable age distribution, so by comparing an observed distribution of ages of individuals in a population, one can see if the population is in a stable age distribution.

Why does the intrinsic rate of increase enter into the formula for the stable age distribution? Think of the case of a population that is doubling every year to help answer this question.

Reproductive value

We have seen that a population does not always grow at a rate given by its ultimate growth rate, the growth rate in the stable age distribution. Is there some quantity that always grows at the same rate? The answer to this question arises from a related question posed and answered by Fisher (1930): what is the contribution of an individual of a given age to the future growth of the population? This will depend not only on the expected number of offspring, but also on when they are born. If the population is

This question is related to the concept of present value from economics.

The 'value' of an offspring is defined as the fraction of the total population size it represents – if the population size doubles, the offspring is worth half as much. This concept makes sense from an evolutionary point of view.

growing, then offspring born sooner are more valuable than off-spring born later, because an offspring born sooner will represent a larger fraction of the population size. In fact, these offspring should be discounted by a factor that is equal to e^{-rt}, where r is the growth rate of the population and t is how far in the future the offspring are born.

Reproductive value of an individual at age x is defined relative to the reproductive value of a newborn, as $v(x)/v(0)$. We first see that the probability of survival from age x to age y is $l(y)/l(x)$, so the expected rate of births to an individual of age x when it is y is $m(y)l(y)/l(x)$. We define the reproductive value of an individual of age x as the sum of all future births, where each future birth is weighted by its value relative to a birth now. We actually perform the sum over all ages, where at each age we use the expected number or rate of births. A birth at age y to an individual that is now x will be counted not as 1, but as $e^{-r(y-x)}$. We thus define

$$\frac{v(x)}{v(0)} = \int_x^\infty e^{-r(y-x)} \frac{l(y)}{l(x)} m(y) dy \tag{2.68}$$

$$\approx \sum_{y=x}^\infty e^{-r(y-x)} \frac{l_y}{l_x} m_y \tag{2.69}$$

$$= \frac{\sum_{y=x}^\infty e^{-ry} l_y m_y}{e^{-rx} l_x}. \tag{2.70}$$

So for the vole example, if $x = 2$, to find the value of v_2/v_0 we use the sum

$$\sum_{y=2}^{9} e^{-ry} l_y m_y = e^{-2r} l_2 m_2 + e^{-3r} l_3 m_3 + \ldots + e^{-9r} l_9 m_9. \tag{2.71}$$

and divide it by $e^{-2r} l_2$.

We have computed the reproductive value for the vole population and listed the values in Table 2.4. From the table we observe some general properties of the reproductive value. The reproductive value typically increases from birth, reaches a maximum between the ages of first and maximal reproduction, and then declines.

Thus, the potential future population size is strongly influenced by the current age distribution of individuals in a population.

The word 'discount' emphasizes the analogy with economics, where the term discount rate is used. You may be familiar with the idea of paying less than \$50 for a \$50 savings bond that matures in the future.

To derive (2.70), notice that we can move the terms involving x outside the summation sign. The resulting equation is easier to use in calculations, as in Table 2.4.

The notation v_0/v_0 suggests that the value should be 1. Convince yourself that this is true from the formula (2.68).

Common sense indicates this is true. A human population with an excess (compared to the stable age distribution) of younger individuals will eventually be larger than a population that initially is the same size but starts off with more older individuals.

Problems

1. Evans and Smith (1952) calculated r for the human louse and found it to be approximately 0.1 per day. Use the equation

$$N(t) = N(0)e^{rt} \qquad (2.72)$$

and rearrange to get

$$\frac{\ln[N(t)/N(0)]}{r} = t. \qquad (2.73)$$

Using this equation, if we know r, $N(0)$, and $N(t)$, we can find t.

Starting with 10 lice, how long will it take for an exponentially growing population of lice to reach 100? 1,000? 100,000,000? 100,000,000,000? Does this surprise you? Discuss.

2. In a population (of an imaginary organism that lives 2 years), the average number of births for 1-year-olds is 1/2, the average number of births for 2-year-olds is 2, and the survival probability from 1 to 2 is 1/2. Death is certain after 2 years.

   (a) Set up a Leslie matrix model for this population.

   (b) If the population starts with 1 adult and no juvenile, find the number of juveniles, adults, and the total population after 3 years. Do the same if the population starts with no adults and 1 juvenile. Who seems to be 'worth' more, in terms of future population size – adults or juveniles?

   (c) Find the long-term growth rate (largest eigenvalue) and the stable age distribution (corresponding eigenvector, the ratio of 1-year-olds to 2-year-olds) for this population. Compare and contrast these numbers to your findings for part (b).

3. Compute

$$\begin{pmatrix} 1 & 2 \\ -3 & 4 \end{pmatrix}\begin{pmatrix} 2 \\ 5 \end{pmatrix}.$$

4. For many bird species, the fecundity and survivorship of adults is independent of the age of the adult bird. Thus, we can think of the population as composed of two classes, juveniles and adults. As in the Leslie matrix, we focus only on females. Set up a model based on a 2 × 2 matrix to describe the dynamics of a bird population without density dependence.

5. Given the following values of l_x and m_x, find r accurate to two decimal places (try different values of r in Euler's equation – if the sum is too large, try a larger value of r; if it is too small, try a smaller value of r):

x	l_x	m_x
0	1.0	0
1	0.6	0
2	0.5	0
3	0.4	3
4	0.3	4
5	0	0

Compute the stable age distribution c_x and the reproductive value v_x for this population, and graph them against the age x. For what age x is v_x maximized? Why?

6. This will require either a spreadsheet or some computer programming. For the snapping turtle life table given in Table 2.3, find r. Then compute the stable age distribution c_x and the reproductive value v_x/v_0 for this population and graph them against the age x. What can you conclude from the graph of the reproductive value?

7. Find an article containing a life table in a recent issue of *Ecology, Ecological Applications, Journal of Animal Ecology, Journal of Ecology*, or *Conservation Biology*. Compute r and compare it to the number in the article. Also, compute the stable age distribution.

Suggestions for further reading

For an in-depth discussion of age-structured population growth, see Caswell (1989). Leslie's (1945, 1948) original papers are worth reading, although they are complex and we now do these computations differently.

An extended discussion of life tables and survivorship curves is in the book by Hutchinson (1978). Numerous examples of life tables are presented in Andrewartha and Birch (1954). Computation of growth rates from life tables has played a role in many discussions in conservation biology; many examples have been discussed in the journal *Conservation Biology*. For example, see the paper by Congdon et al. (1993) on Blanding's turtles.