

Problems

- 2.1. Suppose a population of butterflies is growing according to the logistic equation. If the carrying capacity is 500 butterflies and $r = 0.1$ individuals/(individual • month), what is the maximum possible growth rate for the population?
- 2.2. A fisheries biologist is maximizing her fishing yield by maintaining a population of lake trout at exactly 500 individuals. Predict the initial instantaneous population growth rate if the population is stocked with an additional 600 fish. Assume that r for the trout is 0.005 individuals/(individual • day).
- 2.3. You are studying a density-dependent turtle population that has the following relationships for the birth rate b' and the death rate d' as a function of population size (N):
- $$b' = 0.10 + 0.03N - 0.0005N^2$$
- $$d' = 0.20 + 0.01N$$
- Plot these functions in the same graph and discuss the population dynamics of the turtle. How does this model differ from the simple logistic model with linear birth and death functions?
- *2.4. Prove that the decline of a population above its carrying capacity is always faster than the corresponding increase below carrying capacity. (Hint: The starting population above carrying capacity should be represented as $K + x$.)
- *2.5. In our derivation of the logistic equation, we assumed that both the birth and the death rates were density-dependent. Prove that the logistic model holds for a population in which the birth rate is density-dependent and the death rate is density-independent. Use the same approach as in Expressions 2.1 to 2.9.
- *2.6. Tropical populations of many organisms experience seasonal variation in rainfall and food supply, even though temperatures are fairly constant year-round. Suppose that a water-filled tropical tree hole has a carrying capacity of 500 mosquito larvae. The water level in the hole declines gradually through the dry season, so the carrying capacity varies seasonally between 250 and 750 larvae. If the population is slow-growing, what is the long-term average population size, and what sort of temporal fluctuations in population size would you expect to see? Assume that $rc \ll 1.0$.

* Advanced problem

CHAPTER 3

Age-Structured Population Growth



Model Presentation and Predictions

EXPONENTIAL GROWTH WITH AGE STRUCTURE

In Chapter 1, we represented per capita birth and death rates as constants (b and d), which allowed us to easily calculate r for a population with exponential growth. The resulting model was appropriate for “simple” organisms such as single-celled bacteria or protozoa. But for most plants and animals, birth and death rates depend on the age of an individual.

For example, a newborn elephant cannot reproduce immediately, but must grow for a decade or more before it is reproductively mature. Death rates also vary with age. Seeds, larvae, and hatchlings usually have higher mortality rates than older age classes. Death rates also tend to be high for the very oldest individuals in a population, which may be more vulnerable to predators, parasites, and disease.

The age structure of a population has the potential to affect population growth. For example, if a population consisted only of tadpoles, it would not begin to grow until the tadpoles had metamorphosed into frogs and reached sexual maturity. In contrast, if a population of monkeys consisted only of old, postreproductive individuals, it would decline to extinction.

In this chapter, we will learn how to calculate r for a population in which birth and death rates depend on the age of an organism. Next, we will illustrate the short-term changes in age structure of a population that occur before it settles into a pattern of steady exponential growth. We will briefly consider the problem of life history strategies—why natural selection tends to favor certain birth and death schedules. Finally, we will develop a model of population growth for organisms with complex life histories, such as corals and perennial plants, that do not exhibit simple age structure.

Many students find the analysis of life tables to be one of the most confusing topics in ecology. Admittedly, the calculations in this chapter are tedious; we have to keep track of the birth rate, death rate, and number of individuals in each age class of the population. Be careful with your subscripts, but try not to get bogged down in notation. Keep in mind that we are still using a simple model of exponential growth in an environment with unlimited resources. In that sense, the concepts presented in this chapter are no different than those in Chapter 1.

NOTATION FOR AGES AND AGE CLASSES

To begin our analysis, we need some notation to keep track of the different ages and age classes in a population. Technically, we are modeling a population with continuous births and deaths. However, because we are classifying individuals into discrete age classes, our calculations will represent approximations to continuous growth. There is more than one way to approximate

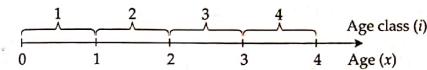


Figure 3.1 The relationship between age (x) and age class (i) in population growth models. (From Caswell 2001.)

these continuous functions, and the equations we use depend on the timing of the population censuses and the seasonal pattern of births and deaths.

We use the variable x in parentheses to refer to the age of an individual. For our discussion, the units of x will be years. However, any convenient time interval can be used, and the choice will usually be based on the life span of the organism and the type of census data that are available. By convention, we classify a newborn as age 0 (not age 1). An individual is age 0 at birth, age 0.5 at 6 months, and age 1 at its first birthday, which is the start of the second year. We use the constant k to refer to the final age in the life table, that is the age by which all individuals have died. Thus, x is a number whose value ranges from 0 to k . The number of ages in the life table depends on the length of the census interval and the life span of the organism.

Alternatively, we can designate the age of an individual by its age class. An individual in age class i is between the ages of $i - 1$ and i (Figure 3.1). For example, an individual in the third age class is between the ages of 2 and 3. Similarly, a newborn is of age 0, but is in the first age class. If the ages in the population range from 0 to k , the age classes range from 1 to k . To keep the distinction clear, variables that indicate age will appear in parentheses, whereas variables that indicate age class will be designated by a subscript. For example, $f(5)$ indicates individuals of age 5, whereas f_5 indicates individuals in the fifth age class (those between the ages of 4 and 5).*

There is a subtle distinction between ages and age classes. In a continuously growing population, individuals of different ages have different birth and death rates. However, when we classify individuals into discrete age classes, we will usually be grouping individuals of slightly different ages. For example, the first age class includes both newborns and individuals who are about to celebrate their first birthday. For modeling purposes, we treat both kinds of individuals as identical and assign a single value of survival probability (P_i) and fecundity coefficient (F_i) to all individuals of an age class.

We can analyze our demographic model using the notation of either ages or age classes. We will follow the textbook tradition of using the age notation to describe the life-table analysis. However, we will switch to the age class notation to describe population growth and the analysis of complex life cycles.

*Most ecology textbooks designate ages with subscripts, but I have followed the mathematicians' convention of using subscripts for age-class matrices (see Caswell 2001).

THE FECUNDITY SCHEDULE [$b(x)$]

The **fecundity schedule** consists of the average number of female offspring born per unit time to an individual female of a particular age. The fecundity schedule is a column of values represented as $b(x)$ or $m(x)$, abbreviations for birth or maternity. For example, if $b(6) = 3$, a female of age 6 will give birth to an average of 3 female offspring. Thus, the $b(x)$ schedule gives per capita fecundity rates for females. Technically, we should be modeling the numbers of both males and females, because the two sexes often have different mortality schedules. However, we can reasonably model population growth by counting only the females.

The entries in the fecundity schedule are non-negative real numbers. An entry of zero in the fecundity schedule means that individuals of a particular age do not reproduce. The fecundity schedule gives the *average* reproduction for a female of a particular age, so these numbers do not have to be integers, and may be less than 1.0 for ages with very little reproduction.

Table 3.1 gives a hypothetical life table for an organism that lives to the end of its fourth year. The ages are 0 through 4, and the age classes are 1

Table 3.1 Standard life-table calculations.^a

x	$S(x)$	$b(x)$	$I(x) = S(x)/S(0)$	$g(x) = I(x+1)/I(x)$	$I(x)b(x)$	$I(x)b(x)x$	Initial estimate $e^{-rx}I(x)b(x)$	Corrected estimate $e^{-rx}I(x)b(x)$
0	500	0	1.0	0.80	0.0	0.0	0.000	0.000
1	400	2	0.8	0.50	1.6	1.6	0.780	0.736
2	200	3	0.4	0.25	1.2	2.4	0.285	0.254
3	50	1	0.1	0.00	0.1	0.3	0.012	0.010
4	0	0	0.0		0.0	0.0	0.000	0.000
$R_0 = \frac{\sum I(x)b(x)}{\sum I(x)}$		= 2.9			$\Sigma = 4.3$	$\Sigma = 1.077$		$\Sigma = 1.000$

$G = \frac{\sum I(x)b(x)x}{\sum I(x)b(x)}$	= 1.483 years
$r (\text{estimated}) = \ln(R_0)/G$	= 0.718 individuals/(individual • year)
Correction added to estimated r	= 0.058
$r (\text{Euler})$	= 0.776 individuals/(individual • year)

^a The x , $S(x)$, and $b(x)$ columns are supplied. All others are calculated from these.

through 4. We will use the data in Table 3.1 to illustrate all the calculations necessary for a typical life-table analysis. If you look at the $b(x)$ column, you see that newborns do not reproduce. One-year-olds produce an average of 2 offspring, two-year-olds produce 3 offspring, and three-year-olds produce 1 offspring.

FECUNDITY SCHEDULES IN NATURE

In nature, what sorts of fecundity schedules do we find? Animal ecologists distinguish between **semelparous** and **iteroparous** reproduction. Plant ecologists use the equivalent terms **monocarpic** and **polycarpic**. In semelparous (monocarpic), or “big bang” reproduction, an organism reproduces only once in its lifetime. Examples are oceanic salmon and many flowering desert plants. The fecundity schedule for a semelparous organism would have zeroes for all ages except for the single reproductive age. In iteroparous (polycarpic) reproduction, the individual reproduces repeatedly during its lifetime. Examples include long-lived organisms such as sea turtles and oak trees. Fecundity schedules for iteroparous organisms have non-zero entries for two or more ages.

Plant ecologists use two similar terms, **annual** and **perennial**, to refer to plants that complete their life cycle in a single season, and those that live for more than one season. Although there are many exceptions, most annual species are semelparous, and most perennial species are iteroparous. We will postpone our discussion of the evolutionary significance of these reproductive strategies. For now, we will simply use the fixed fecundity schedule for a population to help us calculate the intrinsic rate of increase.

THE SURVIVORSHIP SCHEDULE [$I(x)$]

Fecundity is only half the story. The population growth rate depends equally on the rates of mortality for different ages. Individuals of a particular age might produce dozens of offspring, but if very few individuals survive to that age, the effect on population growth rate will be minor.

How can we measure the survivorship schedule of a population? Imagine that we have a **cohort** of individuals that were all born at the same time. We follow this cohort from birth until all the individuals have died. We keep track of the number of individuals that have survived to the start of each new year. These data can be represented as a column of numbers, $S(x)$, the **cohort survival**. Table 3.1 gives some cohort data for our hypothetical life table. We begin with a cohort of 500 individuals at birth, and by the beginning of the fifth year, all of them have died.

The raw data in the $S(x)$ column must now be converted to the **survivorship schedule**, designated as $I(x)$, where I stands for life table. The quantity $I(x)$ is defined as the proportion of the original cohort that survives to the start

of age x . Equivalently, we can think of $l(x)$ in terms of the survivorship of an individual. $l(x)$ is the probability that an individual survives from birth to the beginning of age x . To calculate $l(x)$, divide the number of survivors of age x [$S(x)$] by the size of the original cohort [$S(0)$]:

$$l(x) = \frac{S(x)}{S(0)} \quad \text{Equation 3.1}$$

The first entry in the $l(x)$ column is $l(0)$. It represents the survivorship of the cohort to birth. By definition, all individuals in the cohort have "survived" to the start, so the value of $l(0)$ is always 1.0 [$l(0) = S(0)/S(0) = 1.0$]. The last entry in the $l(x)$ column is $l(k)$. It represents the age that none of the original cohort reaches: $l(k)$ always equals 0.0 [$l(k) = 0.0/S(0) = 0.0$]. Between these endpoints, $l(x)$ shrinks in size as individuals in the cohort age and die. Thus, the $l(x)$ column is a set of consecutively decreasing real numbers between 1.0 and 0.0.

For the data in Table 3.1, the original cohort was 500 individuals, so we will divide each observation by this value to calculate $l(x)$. Notice that 80% of the original cohort survived to age 1 [$l(1) = 0.80$], but only 10% of the cohort made it to the start of age 3 [$l(3) = 0.10$]. This remaining 10% died between age 3 and age 4, so $l(4) = 0.0$; none of the original cohort is left.

When you calculate $l(x)$ from a survivorship schedule, take care to divide all the entries by the original cohort size [$S(0)$]. Do not make the common mistake of dividing $S(x)$ by other values in the life table. In the next section, we will calculate age-specific survival probabilities, which do use consecutive values of $S(x)$. But for the calculation of $l(x)$, always divide the observed values by $S(0)$.

SURVIVAL PROBABILITY [$g(x)$]

The survivorship schedule $l(x)$ gives the probability of survival from birth to age x . To compare the survival of different ages directly, we must determine the probability of survival from age x to age $x + 1$, given that an individual has already survived to age x . The **survival probability** $g(x)$ is the probability that an individual of age x survives to age $x + 1$:

$$g(x) = \frac{l(x+1)}{l(x)} \quad \text{Equation 3.2}$$

From Table 3.1, for example, the probability that a newborn survives its first year and reaches age 1 is $g(0) = 0.8/1.0 = 0.8$. Thus, there is an 80% chance that a newborn will still be alive at age 1. If we are thinking in terms of a

cohort analysis, 80% of all newborns will be alive at age 1. In contrast, the probability of survival between ages 1 and 2 [$g(1)$] is $(0.4/0.8) = 0.5$. Although the $l(x)$ schedule never increases with age, the $g(x)$ schedule may either increase or decrease. The way in which survival probabilities change with age is an important component of the life history of an organism, as described in the next section.

SURVIVORSHIP SCHEDULES IN NATURE

What are the different types of survivorship curves observed in nature? There are three basic patterns. These can be seen by plotting the logarithm of $l(x)$ on the y axis and age (x) on the x axis. The points on this graph are connected to form a survivorship curve. The slope of this curve at any point is $\ln[g(x)]$. Therefore, if the survivorship curve forms a straight line, the probability of survival is constant over those ages.

Figure 3.2 illustrates the three types of curves. A **Type I survivorship curve** has high survivorship during young and intermediate ages, then a steep drop-off in survivorship as individuals approach the maximum life span. Examples include humans and other mammals that invest a good deal of

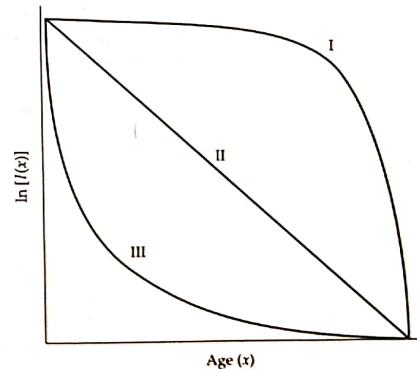


Figure 3.2 Type I, II, and III survivorship curves. Note the logarithmic transformation of the y axis.

parental care in their offspring, ensuring high survivorship of young age classes.

The opposite, and more common, pattern is a **Type III survivorship curve**. In this case, survivorship is very poor for the young age classes, but much higher for older individuals. Examples include many insects, marine invertebrates, and flowering plants. These organisms may produce hundreds or thousands of eggs, larvae, or seeds, most of which die. However, the handful of individuals that do pass through this vulnerable stage have relatively high survivorship in later years.

Finally, the **Type II survivorship curve** is intermediate between these two. Because it is a straight line on a logarithmic graph, the Type II survivorship schedule is one in which the mortality rate is constant throughout life. Few organisms have a true Type II survivorship curve, because it is unusual for the probability of death to remain constant as an organism ages. Some birds have a Type II curve for much of their lives, but often with a steeper mortality curve during the more vulnerable egg and chick stages.

The $l(x)$ and $b(x)$ schedules are the basis for all our life-table calculations. Keep in mind that these schedules are independent pieces of data about death and birth. The $l(x)$ schedule is calculated by following the survivorship of a cohort of organisms. It tells us only the chances of individuals surviving to a particular age, and contains no information about their reproduction. In contrast, the $b(x)$ schedule reveals only the per capita birth rates of females of different ages, and does not say anything about how many females actually survive to those ages. If we know the $l(x)$ and $b(x)$ schedules, we can calculate the intrinsic rate of increase, as illustrated in the next section. When you work with the $l(x)$ and $b(x)$ schedules, be careful with your notation. Remember that the $l(x)$ column gives the survivorship *up to* the start of age x , whereas the $b(x)$ schedule gives the per capita birth rates of females of age x .

CALCULATING NET REPRODUCTIVE RATE (R_0)

To estimate r from the $l(x)$ and $b(x)$ schedules, we first have to compute two other numbers, the net reproductive rate (R_0) and the generation time (G). These numbers are part of the recipe for estimating r , but they tell us important things about an age-structured population in their own right. The **net reproductive rate**, R_0 , is defined as the mean number of female offspring produced per female over her lifetime. To compute R_0 , multiply each value of $l(x)$ by the corresponding value of $b(x)$ and sum these products across all ages:

$$R_0 = \sum_{x=0}^k l(x)b(x) \quad \text{Equation 3.3}$$

The units of R_0 are numbers of offspring. The net reproductive rate represents the reproductive potential of a female during her entire lifetime, adjusted for the mortality schedule. Suppose that there was no mortality in the population until females reached their maximum age. This would mean that $l(x) = 1.0$ for all ages except the last. In this case, Equation 3.3 would simply add up the lifetime production of offspring—the gross reproductive rate. But in most populations, mortality in each age class reduces the potential contribution of offspring to the next generation. Thus, the net reproductive rate is the offspring production discounted by mortality. For the fecundity and survivorship schedules in Table 3.1, $R_0 = 2.9$ offspring.

If R_0 is greater than 1.0, there is a net surplus of offspring produced each generation, and the population increases exponentially. If R_0 is less than 1.0, the mortality is so great that the population cannot replace itself, and it declines to extinction. Finally, if $R_0 = 1.0$, the offspring production exactly balances the mortality each generation, and the population size does not change.

This description of R_0 is very similar to the description of λ , the finite rate of increase in the exponential growth model (see Chapter 1). In fact, you might be tempted to conclude that $r = \ln(R_0)$, because $r = \ln(\lambda)$ for populations with no age structure (Equation 1.5). However, λ measures the rate of increase as a function of *absolute time*, whereas R_0 measures increase as a function of *generation time*. Therefore, if we want to calculate r , we must scale R_0 to account for generation time.

CALCULATING GENERATION TIME (G)

Generation time is a somewhat elusive concept for populations with continuous growth. Imagine that we followed a cohort from birth and kept track of all the offspring it produced. One definition of the generation time is the average age of the parents of all the offspring produced by a single cohort (Caughley 1977). This is calculated as:

$$G = \frac{\sum_{x=0}^k l(x)b(x)x}{\sum_{x=0}^k l(x)b(x)} \quad \text{Equation 3.4}$$

The units of $l(x)$ and $b(x)$ cancel in the numerator and denominator, leaving us with an answer in units of time (x). Unless newborns have high fecundity ($b(0) >> 0$), the numerator will always be larger than the denominator in Equation 3.4. Consequently, the generation time will usually be greater than 1.0 for populations with age structure. For the data in Table 3.1, $G = 1.483$ years.

CALCULATING INTRINSIC RATE OF INCREASE (r)

We can use the equation for exponential growth to solve for r in terms of R_0 and G (Mertz 1970). Imagine a population is growing exponentially for a time G :

$$N_G = N_0 e^{rG} \quad \text{Expression 3.1}$$

Dividing both sides by N_0 gives:

$$\frac{N_G}{N_0} = e^{rG} \quad \text{Expression 3.2}$$

The ratio on the left side of the expression is an approximation to the net reproductive rate, R_0 :

$$R_0 \approx e^{rG} \quad \text{Expression 3.3}$$

Taking the natural logarithm of both sides gives:

$$\ln(R_0) \approx rG \quad \text{Expression 3.4}$$

Rearranging Expression 3.4 gives us an approximation for r :

$$r \approx \frac{\ln(R_0)}{G} \quad \text{Equation 3.5}$$

Thus, the rate of population increase is slower for organisms with long generation times. Continuing with the data in Table 3.1, the estimate of r is 0.718 individuals/(individual · year).

Equation 3.5 is only an approximation, although it is usually within 10% of the true value (Stearns 1992). To obtain an exact solution for r , you must solve the following equation:

$$1 = \sum_{x=0}^k e^{-rx} l(x) b(x) \quad \text{Equation 3.6}$$

Equation 3.6 is adapted from the **Euler equation** (pronounced “oiler”), named after the Swiss mathematician Leonhard Euler (1707–1783), who developed it in his analyses of human demography. Later in this chapter, we will illustrate the derivation of the Euler equation. For now, we will simply use Equation 3.6 as a formula for determining the precise value of r .

Because we know the $l(x)$ and $b(x)$ schedules, the only unknown quantity in Equation 3.6 is r . Unfortunately, there is no way to solve this equation except by plugging in different values of r and adjusting your estimate upwards or downwards. A good starting place is the estimate of r from Equation 3.5. For

the data in Table 3.1, substituting $r = 0.718$ into Equation 3.6 gives a sum of 1.077, whereas the correct value of r will generate a sum of exactly 1.0. This calculation indicates that our original estimate of r was too small. Because we are summing with the negative exponent of r , a larger value of r will generate a smaller sum. If we experiment with different values, we find that an r of 0.776 is a close solution to the Euler equation.

DESCRIBING POPULATION AGE STRUCTURE

Once we have calculated r from the fecundity and survivorship schedules, we can forecast the total population size by using any of the equations for exponential growth from Chapter 1. But we are also interested in knowing the number of individuals in each age class of the population. This means we will shift our notation from ages to age classes.

We will use $n_i(t)$ to indicate the number of individuals at time t in age class i . For example, if $n_1(3) = 50$, there are 50 individuals in the first age class at the third time step. Because there are k age classes in the population, the age structure at time t consists of a vector of abundances. We indicate this vector with a boldfaced, lowercase \mathbf{n} :

$$\mathbf{n}(t) = \begin{pmatrix} n_1(t) \\ n_2(t) \\ \vdots \\ n_k(t) \end{pmatrix} \quad \text{Expression 3.5}$$

For example, the vector for the population in Table 3.1 after five years might be:

$$\mathbf{n}(5) = \begin{pmatrix} 600 \\ 270 \\ 100 \\ 50 \end{pmatrix} \quad \text{Expression 3.6}$$

Thus, there are 600 individuals in the first age class, but only 50 individuals in the terminal age class (age class 4). Using information in the mortality and fertility schedules, we can predict how the age structure of a population changes from one time period [$\mathbf{n}(t)$] to the next [$\mathbf{n}(t+1)$].

Describing the population in terms of its age structure requires us to shift from using ages to using age classes. First, we need to obtain **survival probabilities** P_i for each age class. These probabilities represent the chance that an individual in age class i survives to age class $i+1$. Next, we need to calculate **fertilities** F_i for each age class. These fertilities represent the average number of offspring produced by an individual in age class i . Clearly, the survivor-

ship probabilities and fertilities for individuals of different age classes are related to the $l(x)$ and $b(x)$ schedules for individuals of different ages.

However, the conversion of these values is tricky; it depends on the timing of births and deaths within an age class, and the timing of the population census (Caswell 1989). In this primer, we will assume a simple **birth-pulse model**, in which individuals give birth to all their offspring on the day they enter a new age class. We will further assume a **postbreeding census**, in which individuals are counted each year just after they breed.

These assumptions make the calculation of P_i and F_i relatively simple. A **birth-flow model**, in which individuals reproduce continuously in an age class, would require more complex calculations. Keep in mind that the estimates of population growth will depend on how the age-class model is set up. The estimates of population growth also may not match the exact calculations from the Euler equation. Once we have the survival probabilities and fertility values for each age class, we will use them to calculate the changes in population structure with time.

CALCULATING SURVIVAL PROBABILITIES FOR AGE CLASSES (P_i)

For the birth-pulse model with a postbreeding census, the probability that an individual in age class i survives to age class $i + 1$ is:

$$P_i = \frac{l(i)}{l(i-1)} \quad \text{Equation 3.7}$$

This equation is similar to the calculation of the age-specific survival probability $g(x)$ (Equation 3.2), although note the shift in notation as we go to a model of age classes. With Equation 3.7, it is easy to calculate the change in the number of individuals in a particular age class from one time period to the next:

$$n_{i+1}(t+1) = P_i n_i(t) \quad \text{Equation 3.8}$$

Equation 3.8 says that the number of individuals in a particular age class next time step [$n_{i+1}(t+1)$] is the number of individuals currently in the previous age class [$n_i(t)$] multiplied by the survival probability for that age class (P_i). So, the survival probability controls the rate at which individuals "graduate" to each successive age class.

CALCULATING FERTILITIES FOR AGE CLASSES (F_i)

Equation 3.8 works for all age classes except the first. The number of individuals in the first age class depends on the reproduction of all the age classes.

We define the fertility of age class i as:

$$F_i = b(i)P_i \quad \text{Equation 3.9}$$

Equation 3.9 says that the fertility of a particular age class is the number of offspring produced, discounted by the survival probability for that age class. The discount is necessary because the parents must survive through the age class in order to reproduce and have their offspring counted.

Once F_i is known for each age class, we multiply these fertilities by the number of individuals in each age class. This product is then summed over all age classes to calculate the number of new offspring:

$$n_1(t+1) = \sum_{i=1}^k F_i n_i(t) \quad \text{Equation 3.10}$$

Having derived fertility and survivorship coefficients for each age class from the $l(x)$ and $b(x)$ schedules, we can now calculate the number of individuals in each age class for a single time step. For a population with four age classes, we would have:

$$\begin{aligned} n_1(t+1) &= F_1 n_1(t) + F_2 n_2(t) + F_3 n_3(t) + F_4 n_4(t) \\ n_2(t+1) &= P_1 n_1(t) \\ n_3(t+1) &= P_2 n_2(t) \\ n_4(t+1) &= P_3 n_3(t) \end{aligned} \quad \text{Expression 3.7}$$

In the next section we will express these changes in matrix form.

THE LESLIE MATRIX

We can represent the growth of an age-structured population in matrix form. The **Leslie matrix**, named after the population biologist Patrick H. Leslie, describes the changes in population size due to mortality and reproduction (Leslie 1945). If there are k age classes, the Leslie matrix is a $k \times k$ square matrix. It always has the following form:

$$A = \begin{bmatrix} F_1 & F_2 & F_3 & F_4 \\ P_1 & 0 & 0 & 0 \\ 0 & P_2 & 0 & 0 \\ 0 & 0 & P_3 & 0 \end{bmatrix} \quad \text{Expression 3.8}$$

Each column of the Leslie matrix is the age at time t and each row is the age at time $t + 1$. Each entry in the matrix represents a transition, or change in the number of individuals from one age class to another. In the Leslie matrix, the

fertilities are always in the first row; they represent contributions to newborns from reproduction of each age class. The survival probabilities are always in the subdiagonal. They represent transitions from one age class to the next. All other entries in the Leslie matrix are 0 because no other transitions are possible. Individuals cannot remain in the same age class from one year to the next, so the diagonals must equal zero. Similarly, individuals cannot skip or repeat age classes, so other entries in the matrix are zero.

The reason for using the matrix format is that we can now describe population growth as a simple matrix multiplication:

$$\mathbf{n}(t+1) = \mathbf{A}\mathbf{n}(t) \quad \text{Equation 3.11}$$

In other words, the population vector in the next time step $[\mathbf{n}(t+1)]$ equals the Leslie matrix (\mathbf{A}) multiplied by the current population vector $[\mathbf{n}(t)]$. The rules of matrix algebra are used to calculate the changes in abundance in each age class, and these are equivalent to the calculations in Expression 3.7. If you have had matrix algebra, λ is the dominant eigenvalue of the Leslie matrix. Now that we have converted our age-based life-table data to an age-class Leslie matrix, we are ready to see how age structure changes during population growth.

Table 3.2 Calculation of age-specific survival probabilities and fertilities for the Leslie matrix. Data from Table 3.1. Notice that the first row of the table is blank for P_i and F_i , because we begin counting age classes at 1, not 0.

x	i	I(x)	b(x)	$P_i = I(i)/I(i-1)$	$F_i = b(i)P_i$
0		1.0	0		
1	1	0.8	2	0.80	1.60
2	2	0.4	3	0.50	1.50
3	3	0.1	1	0.25	0.25
4	4	0	0	0.00	0.00

The resulting Leslie matrix is:

$$\mathbf{A} = \begin{bmatrix} 1.6 & 1.5 & 0.25 & 0 \\ 0.8 & 0 & 0 & 0 \\ 0 & 0.5 & 0 & 0 \\ 0 & 0 & 0.25 & 0 \end{bmatrix}$$

STABLE AND STATIONARY AGE DISTRIBUTIONS

Table 3.2 converts the life-table data of Table 3.1 to a Leslie matrix. We use this Leslie matrix to compare the growth of two hypothetical populations. One population has 50 individuals in each age class, and the second population has 200 newborns, but no other age classes present. Figure 3.3 shows the

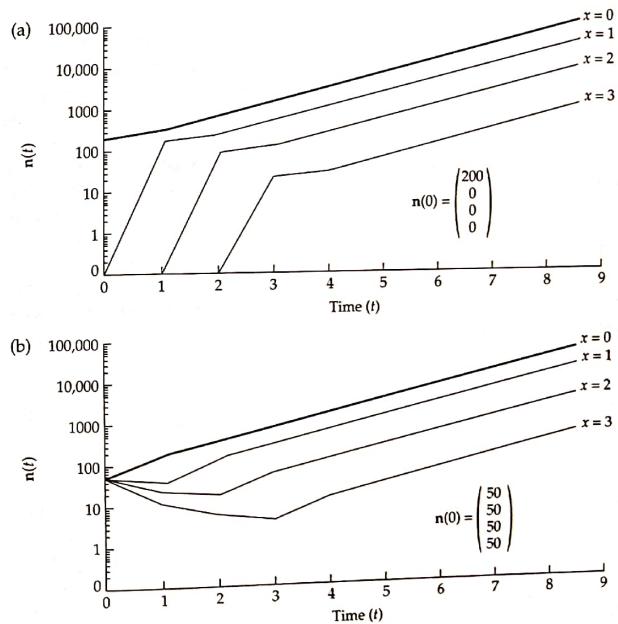


Figure 3.3 Stable age distributions, showing the effects of initial age structure on population growth. Each line represents a different age class, growing according to the birth and death schedules of Table 3.1. In (a), the initial age distribution was 200 newborns. In (b), the initial age distribution was 50 individuals in each age class. After some initial fluctuations, both populations settle into identical stable age distributions. On the logarithmic scale, the straight line for each age class indicates exponential increase.

number of individuals in each age class as a function of time. You can see that the graphs for the two populations initially appear quite different from one another as the relative numbers in the different age classes change in the early phases of population growth. In particular, you can see that the population with 200 newborns is dominated by this single age class, which passes as a cohort through the older age classes. However, after about 6 time steps, both populations have converged on the same age structure—they both have the same relative numbers in each age, with newborns being most common, and the oldest individuals being most rare. These relative proportions are maintained as the numbers in all ages increase exponentially.

These graphs illustrate an important property of age-structured populations. For most life tables, if a population is growing with constant birth and death rates, it will quickly converge on a **stable age distribution**, regardless of its initial age structure. In the stable age distribution, the *relative* numbers of individuals in each age class remain constant. Remember that the *absolute* numbers will increase exponentially, as evidenced by the linear population growth curves on the logarithmic scale of Figure 3.3. A special kind of stable age distribution is the **stationary age distribution**. In a stationary age distribution, $r = 0$, so both the relative and the absolute numbers in each age class remain constant.

What are the relative proportions in the different ages once the stable age distribution has been achieved? The proportion of the population represented by each age is just the number in that age divided by the total population size. This ratio is (Mertz 1970):

$$c(x) = \frac{e^{-rx}l(x)}{\sum_{x=0}^k e^{-rx}l(x)} \quad \text{Equation 3.12}$$

Once r has been calculated from the $l(x)$ and $b(x)$ schedules, Equation 3.12 can be used to determine the stable age distribution. The calculations are illustrated in Table 3.3. In a stable age distribution, newborns are the most common age, and the oldest age is least common. In most cases, the larger r is, the greater the proportion of the total population represented by newborns and young individuals. For the matrix algebra solution, the stable age distribution is the right-hand eigenvector of the Leslie matrix.

The Leslie matrix calculations of population growth can also be used as an independent check on the calculation of r . Table 3.4 illustrates some of the raw data of age structure and population size from Figure 3.3a. For any two consecutive time steps in the model, the ratio of the current population size to the previous population size is a measure of λ , the finite rate of increase. The final column of Table 3.4 gives the natural logarithm of this ratio, which is r .

Table 3.3 Calculation of stable age and reproductive value distributions.^a

x	l(x)	b(x)	Stable age distribution		Reproductive value distribution			
			$l(x)e^{-rx}$	c(x)	$e^{rx}/l(x)$	$e^{-r}l(y)b(y)$	$\sum e^{-r}l(y)b(y)$	v(x)
0	1.0	0	1.000	0.684	1.000	0.000	1.000	1.000
1	0.8	2	0.368	0.252	2.716	0.736	1.000	0.717
2	0.4	3	0.085	0.058	11.802	0.254	0.264	0.118
3	0.1	1	0.010	0.007	102.574	0.010	0.010	0.000
			\sum = 1.463			1.000	y = x \Rightarrow k	

^aThese calculations use $r = 0.776$, from the solution to the Euler equation in Table 3.1.

By 6 or 7 time steps in the model, the stable age distribution has been achieved, and the estimate of r is 0.776, which matches the calculation from the Euler equation in Table 3.1.

Table 3.4 Estimating r from the Leslie matrix calculations.^a

Time step (t)	$n_1(t)$	$n_2(t)$	$n_3(t)$	$n_4(t)$	$n_{\text{total}}(t)$	$\lambda \approx \frac{n_{\text{total}}(t)}{n_{\text{total}}(t-1)}$	$r = \ln(\lambda)$
0	200	0	0	0	200		
1	320	160	0	0	480	2.4	0.875
2	752	256	80	0	1088	2.267	0.818
.
6	16,549	6091	1402	161	24,203	2.173	0.776
7	35,965	13,239	3045	351	52,600	2.173	0.776
8	78,165	28,772	6620	761	114,318	2.173	0.776
.

^aThe data are from different time steps in Figure 3.3a. Fractions for the age-class values have been rounded to the nearest whole number.

Model Assumptions

In spite of the lengthy calculations, the model presented here shares the basic assumptions of the simple exponential growth model we derived in Chapter 1. In other words, we assume a closed population, no genetic structure, and no time lags. In the simple exponential model, we assumed that b and d were constant—they did not vary with time or with population density. In the age-structured model, we assume that the $l(x)$ and the $b(x)$ schedules are constant. As before, if each age class has a constant birth and death rate no matter how large the population, resources must be unlimited.

Incidentally, if we use the value of r from the Euler equation to forecast population growth, we must further assume that the population has achieved a stable age distribution. One final point is that we have described the $l(x)$ schedule from a cohort analysis, in which the fate of a cohort is followed through time. This horizontal, or cohort life table is the simplest method of obtaining the $l(x)$ schedule, but it assumes that death rates are constant during the time the cohort is followed. A more reliable method is to measure short-term death rates directly for each age class. Finally, it is possible to take a cross-section of the population at one time and estimate death rates from the relative sizes of consecutive age classes. This vertical, or static life table is much less reliable and assumes the population has reached a stationary age distribution. However, birth and death rates can be very difficult to measure in the field, and we often have to rely on a number of methods to piece together the data needed for a life-table analysis.

Model Variations

DERIVATION OF THE EULER EQUATION

The Euler equation forms the basis for age-structured demography, so it is important to understand how this equation is derived. The key to the Euler equation is recognizing the relationship between the number of births now and the number of births at some point in the past (Roughgarden 1979). The number of births in the population now, $B(t)$, is simply the sum of the number of births from parents of all different ages:

$$B(t) = \sum_{x=0}^k (\text{births from parents of age } x) \quad \text{Expression 3.9}$$

If we allow the age intervals to become infinitely small, we can express this as an integral equation:

$$B(t) = \int_0^k (\text{births from parents of age } x) dx \quad \text{Expression 3.10}$$

The number of births from parents of age x is the product of the number of

individuals born at time $t - x$, their offspring production [$b(x)$], and their probability of surviving to age x [$l(x)$]:

$$B(t) = \int_0^k B(t-x) l(x) b(x) dx \quad \text{Expression 3.11}$$

Remember that the number of births comes from a population that is increasing exponentially. Using C as an arbitrary starting population size, we have:

$$B(t) = Ce^{rt} \quad \text{Expression 3.12}$$

Substituting this back into Expression 3.12 yields:

$$Ce^{rt} = \int_0^k Ce^{r(t-x)} l(x) b(x) dx \quad \text{Expression 3.13}$$

Finally, if we divide both sides of Expression 3.14 by Ce^{rt} , we have the Euler equation:

$$1 = \int_0^k e^{-rx} l(x) b(x) dx \quad \text{Equation 3.13}$$

As we noted earlier, the equivalent equation in discrete time is:

$$1 = \sum_{x=0}^k e^{-rx} l(x) b(x) \quad \text{Equation 3.14}$$

REPRODUCTIVE VALUE

Using the Euler equation, we can calculate another useful statistic from the life table—the reproductive value of each age (Fisher 1930). The reproductive value is the relative number of offspring that remain to be born to individuals of a given age. You might think that a newborn individual would have the highest reproductive value because it has not yet produced any offspring. However, its reproductive value is discounted by the fact that it might not achieve its maximum potential lifespan and produce all of its potential offspring. Let $v(x)$ equal the reproductive value for an individual of age x . We can define reproductive value as the following ratio in a stable age distribution (Wilson and Bossert 1971):

$$v(x) = \frac{\text{number of offspring produced by individuals of age } x \text{ or older}}{\text{number of individuals of age } x} \quad \text{Expression 3.14}$$

We can use the Euler equation to quantify the terms in the numerator and the

denominator. For the numerator, we add the terms in the Euler equation from the current age forward:

$$\text{Offspring production} = \int_x^k e^{-ry} l(y) b(y) dy \quad \text{Expression 3.15}$$

For the denominator, the number of individuals in age x is the number born at time x in the past, multiplied by the probability of surviving to age x . Thus:

$$\text{Number in age } x = e^{-rx} l(x) \quad \text{Expression 3.16}$$

Substituting Expressions 3.15 and 3.16 into 3.14 gives:

$$v(x) = \frac{\int_x^k e^{-ry} l(y) b(y) dy}{e^{-rx} l(x)} \quad \text{Expression 3.17}$$

Rearranging the right-hand side yields a formula for reproductive value:

$$v(x) = \frac{e^{rx}}{l(x)} \int_x^k e^{-ry} l(y) b(y) dy \quad \text{Equation 3.15}$$

The discrete-time version of Equation 3.15 allows us to use the $l(x)$ and $b(x)$ schedules to calculate the reproductive value for individuals of age x :

$$v(x) = \frac{e^{rx}}{l(x)} \sum_{y=x+1}^k e^{-ry} l(y) b(y) \quad \text{Equation 3.16*}$$

For the matrix algebra solution, the left-hand eigenvector of the Leslie matrix is the vector of reproductive values. From Equation 3.15, the reproductive value of newborns always equals 1.0 ($v(0) = 1.0$). Thus, reproductive value is measured relative to that of the first age. For example, if $v(3) = 2.0$, an individual of age 3 will produce roughly twice as many offspring during the remainder of its lifetime as will a newborn. Reproductive value reflects the survivorship of an individual to its current age, its survivorship and reproduction in future ages, and the magnitude of r . Reproductive value usually peaks at or near the age of first reproduction, then drops off rapidly with later ages. For the data in Table 3.1, reproductive value is maximal for individuals of age 0 (Table 3.3).

*Be careful with the notation in this formula. In particular, notice that the summation subscript ($y = x + 1$) is increased by one. Thus, using the data from the sixth and eighth columns of Table 3.3, $v(1) = (2.716)(0.264) = 0.717$. Equation 3.16 generates reproductive values that are consistent with the matrix algebra solutions, but the formula is restricted to birth-pulse populations with a post-breeding census. See Goodman (1982) and Caswell (2001) for more details.

Reproductive value tells us which ages in the population are most "valuable" for future population growth. In Chapter 2, we noted that maximum yield for a harvested population occurred when the population was harvested to maximize population growth rate. For the simple logistic model, the best strategy turned out to be maintaining the population at $K/2$. For an age-structured population, maximizing population growth rate would mean harvesting individuals with relatively low reproductive value—usually newborns and very old individuals, depending on the age structure of the population.

Reproductive value is also relevant to problems of population management and conservation biology. If we are going to transplant captive-bred individuals to a new population in order to increase the population growth rate, we should wait until those individuals reach the age with the highest reproductive value. Finally, natural selection will operate most heavily on ages with high reproductive value. For example, an allele that expresses deleterious effects in reproductive age classes will be eliminated by selection much more quickly than an allele that expresses the effects in older age classes, with lower reproductive value. **Senescence** may represent the accumulation of deleterious effects in old individuals. Selection pressure is weaker on older individuals (Rose 1984), in part because of their lower reproductive value (Fisher 1930).

LIFE HISTORY STRATEGIES

Life-table data are essential for ecological predictions of population growth rates and age structure. From an evolutionary perspective, we can ask why we see certain life history patterns. In other words, why has natural selection favored certain $l(x)$ and $b(x)$ schedules? Selection will favor any life history schedule that maximizes an individual's contribution of offspring to the next generation. Thus, the "perfect" life history schedule would be one with maximum survivorship and maximum fertility in all age classes!

However, two forces prevent the evolution of this optimal life history. First, we expect a number of **tradeoffs** to occur among life history traits. Organisms that invest heavily in reproduction have less energy to devote towards growth, maintenance, and resource acquisition. This may lead to tradeoffs between reproduction and survivorship. An organism may produce many small offspring that survive poorly or a few large offspring that survive well. Hence, there may be tradeoffs between offspring number and offspring survivorship.

Life history strategies will also be shaped by **constraints**—physiological or evolutionary limitations that prevent the evolution of certain life history traits. For example, organisms with large body size must take longer to grow and reach maturity, so the age at first reproduction may be constrained by body size. If an organism bears live offspring, body size will also constrain the num-

ber of offspring produced. The life history traits of an organism may reflect a long evolutionary heritage, and may not represent the best "solution" to the problem of maximizing fitness in the organism's current environment.

One popular body of theory envisions that relative population density serves as an important selective force on life history traits (MacArthur and Wilson 1967; Pianka 1970). The theory of ***r*-K selection** takes its name from the two constants of the logistic growth equation. Imagine a population that is maintained at low population density, so that resources for growth are not limited. Under these circumstances, the best reproductive strategy is simply to maximize offspring production. So, the traits expected under *r*-selection are early, semelparous reproduction, large *r*, many offspring with poor survivorship, a Type III survivorship curve, and small adult body size.

By contrast, in *K*-selection, an organism is growing in an environment that is chronically crowded. An *r*-strategy will not work in this case because the offspring will face limited resources and be relatively poor competitors. Instead, the best strategy is one that leads to fewer, high-quality offspring that are superior competitors. With resource limitation, *K*-selection should favor late, iteroparous reproduction, small *r*, few offspring with good survivorship, a Type I survivorship curve, and large adult body size. Classic examples of species thought to have evolved under the different regimes include mosquitoes and weeds (*r*-selected), and humans and whales (*K*-selected).

In spite of its popularity in textbooks, the theory of *r*- and *K*-selection is beset by a number of problems. One fundamental problem is that the "predictions" of *r*-*K* selection theory were never derived from a population model with age structure. Another difficulty is that population density is not the only force driving the evolution of life history traits. For example, the theory predicts that iteroparity evolves when organisms face resource competition and must devote more of their energy to growth and maintenance than to reproduction. But iteroparity could also evolve as a "bet-hedging" strategy if the survival of offspring is uncertain from one time period to the next (Murphy 1968). It may be advantageous to spread reproduction over many time periods if there is a risk of losing all your offspring if they are born at the wrong time.

Moreover, not all organisms have life history traits that neatly fit the predictions of the model. For example, many forest trees are long-lived and iteroparous (*K*-selection), but they have a Type III survivorship curve (*r*-selection). Finally, the *r*-*K* selection theory has not been confirmed experimentally. Laboratory populations of fruit flies (Taylor and Condra 1980) and protzoa (Luckinbill 1979) did not always evolve *r*-selected traits when they were maintained in uncrowded conditions or *K*-selected traits when they were maintained in crowded conditions. Although the original theory of *r*-*K* selection has been discarded, it is nevertheless true that the ecological conditions

an organism experiences—including its population density—can be important forces of natural selection that shape life histories.

For example, mortality from predators can lead to major changes in birth and death schedules (Gadgil and Bossert 1970; Roff 1992). If predators specialize on adult size classes, natural selection will favor individuals that mature early and reproduce at small body sizes. These predictions have been confirmed for freshwater tropical guppies: life histories differ among populations of the same species, depending on whether or not predators are present (Reznick et al. 1996). Moreover, field studies demonstrate that life history traits can evolve very rapidly in response to the presence of predators (Reznick et al. 1997). Other studies have shown that body size—and hence some life history traits—can also evolve in response to the presence of competing species (Schlüter 1994). In Chapters 5 and 6, we will develop ecological models for understanding the effects of predators and competitors on population dynamics. But it is important to emphasize that these interactions have consequences for the evolution of life histories as well.

STAGE- AND SIZE-STRUCTURED POPULATION GROWTH

An implicit assumption in our development of the life table model is that the age of an organism is the "correct" variable to use in defining the life history. But for many life histories, age is not the critical variable. For example, many insects pass through egg, larval, pupal, and adult stages. Survival may be influenced more by an insect's stage than its age. That is, survival of a beetle may not depend on whether the beetle is three or six months old, but on whether it is in the larval or adult stage. Of course, age and stage are not independent of one another, because an organism's life history stage will depend, in part, on how old it is. But the transitions between stages are often flexible and depend on biotic factors, such as food supply and population density, and abiotic factors, such as temperature and photoperiod.

Even for organisms that do not have distinct life history stages, survival and reproduction may depend more on the size or an organism than on its age. Many organisms have indeterminate growth—a small fish may be either a fast-growing juvenile or a stunted adult. If the risk of mortality is from predation by other fishes, only the individual's size, rather than its age, may be relevant. Finally, "modular" organisms such as plants and corals may be organized as colonies or semi-independent units (plant shoots) that are capable of reproduction. In these cases, the life history may be extremely complex, as coral colonies can fragment or fuse, and plants can reproduce through vegetative propagation. In all these examples, the age of the organism is less important than its size or stage in determining its survivorship and reproduction.

Fortunately, the Leslie matrix can be modified to account for these kinds of life histories (Lefkovitch 1965). The key change is that the entries in the population matrix no longer represent the age of an organism, but rather its stage (or size). We still incorporate a time step that represents the transition from one stage to the next. For example, here is a transition matrix for a simplified insect life cycle with three stages—egg, larva, and adult:

$$\begin{matrix} & \text{egg} & \text{larva} & \text{adult} \\ \text{egg} & 0 & 0 & F_{ae} \\ \text{larva} & P_{el} & P_{ll} & 0 \\ \text{adult} & 0 & P_{la} & P_{aa} \end{matrix} \quad \text{Expression 3.18}$$

Remember that each column represents the stage at time t and each row represents the stage at time $t + 1$. The entries in the first row represent fertilities. The entries in the other rows represent transition probabilities between stages. In contrast to the Leslie matrix, we now have positive entries on the diagonal. This means that larvae and adults can stay in a particular stage at a given time, whereas eggs will either die or advance to the larval stage. Only the adult can reproduce, so there is a single fertility entry (F_{ae}) for this stage.

Here is a transition matrix for a long-lived forest tree that is classified into five size classes:

$$\begin{matrix} & \text{size 1} & \text{size 2} & \text{size 3} & \text{size 4} & \text{size 5} \\ \text{size 1} & P_{11} & F_{21} & F_{31} & F_{41} & F_{51} \\ \text{size 2} & P_{12} & P_{22} & 0 & 0 & 0 \\ \text{size 3} & 0 & P_{23} & P_{33} & 0 & 0 \\ \text{size 4} & 0 & 0 & P_{34} & P_{44} & 0 \\ \text{size 5} & 0 & 0 & 0 & P_{45} & P_{55} \end{matrix} \quad \text{Expression 3.19}$$

Again, there is the possibility that an individual will remain in the same size class (diagonal elements) or grow to the next consecutive size class (subdiagonal elements). All size classes except the first reproduce, giving positive fertility values in the first row of the matrix.

As a final, and more complex, example, consider a population of reef-building corals with three size classes (small, medium, and large):

$$\begin{matrix} & \text{small} & \text{medium} & \text{large} \\ \text{small} & P_{ss} + P_{ss} & P_{ms} + P_{ms} & P_{ls} + P_{ls} \\ \text{medium} & P_{sm} & P_{mm} & P_{lm} \\ \text{large} & P_{sl} & P_{ml} & P_{ll} \end{matrix} \quad \text{Expression 3.20}$$

As before, the diagonal elements represent the probability that a colony remains in the same size class, and the subdiagonal elements represent the probability that a colony grows to the next size class. However, there is now the possibility that large colonies can fragment into medium (P_{lm}) or small (P_{ls}) colonies, and that medium colonies can fragment into small colonies (P_{ms}). Small colonies can also fuse with one another, thus “skipping” a stage and going directly from small to large (P_{sl}). Finally, look at the first row of the matrix and notice that the entries are sums of fertilities and stage transitions. This relationship occurs because the production of small colonies has components of sexual reproduction (F) and asexual fragmentation and persistence (P).

As illustrated in Figure 3.4, these complex life cycles can also be represented in loop diagrams. Each circle in the loop represents a different life his-

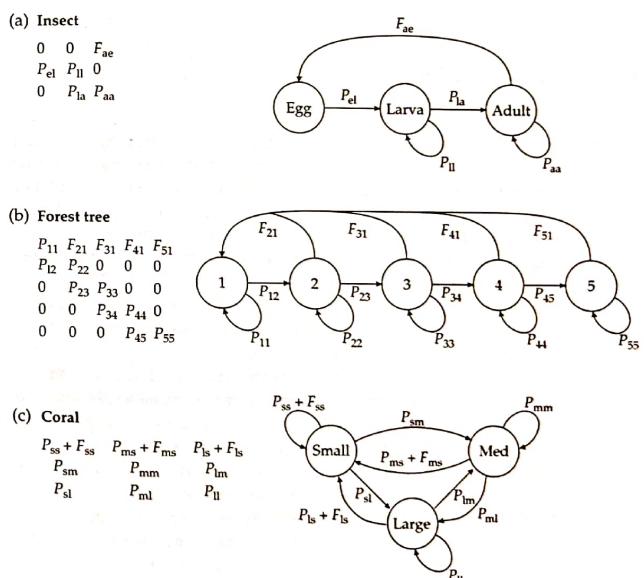


Figure 3.4 Stage-transition matrices and loop diagrams for different life histories. (a) Simplified insect life history. (b) Long-lived forest tree life history. (c) Coral life history, with sexual and asexual reproduction.

tory stage, and each arrow represents a transition from one stage to the next. Stages not connected by arrows have a zero for the corresponding entry in the transition matrix.

In spite of the complexities of these life cycles, the mechanics of the matrix multiplication are exactly the same as for the simple Leslie matrix. As long as the transition elements are constant, the population will eventually exhibit exponential growth and a stable stage distribution. However, we can no longer use the Euler equation for these life histories, and must obtain the matrix solutions for r and the stable stage distribution. For any transition matrix, λ is the dominant eigenvalue. The right-hand eigenvector is the stable stage distribution, and the left-hand eigenvector is the reproductive value distribution (Caswell 1989). The matrix approach allows us to use the same analytical framework to study complex life histories that do not fit a simple age classification.

Empirical Examples

LIFE TABLES FOR GROUND SQUIRRELS

A long-term demographic study of the Uinta ground squirrel (*Spermophilus armatus*) demonstrates the importance of life-table analysis in understanding population growth (Slade and Ralph 1974). At a field station in northern Utah, squirrels emerged from hibernation each year between late March and mid-April, depending on the weather. Females bred shortly after they emerged and established territories. The first young were born in early May, and juveniles left their natal burrows about three weeks later. During June and July, all age classes and sexes in the population were active. Adults began hibernating in July, and by September all squirrels had disappeared underground.

Researchers trapped and tagged all individuals in the 8.9-hectare study area and monitored their activity from observation towers. The research was conducted over a seven-year period and divided into two phases. During the first phase (1964–1968), the population was left undisturbed, except for the monitoring. Population size fluctuated from 178 to 255, with a mean of 205. During the second phase (1968–1971), researchers reduced the squirrel population to about 100 individuals. Life-table analysis (Table 3.5) revealed the dramatic effects of density reduction on growth rate and age structure.

Before the population was reduced, age-specific birth and death rates were approximately balanced, generating a slightly negative growth rate [$r = -0.046 \text{ individuals}/(\text{individual} \cdot \text{year})$]. The maximum life span was approximately five years, although this varied somewhat between different habitats. In the stable age distribution, 37% of the population was juveniles (Figure 3.5a), and reproductive value peaked for individuals during their second year (Figure 3.5b).

Table 3.5 Life tables for Uinta ground squirrels (*Spermophilus armatus*) before and after density reduction.

x (years)	Pre-reduction life table		Post-reduction life table	
	$I(x)$	$b(x)$	$I(x)$	$b(x)$
0.00	1.000	0.00	1.000	0.00
0.25	0.662	0.00	0.783	0.00
0.75	0.332	1.29	0.398	1.71
1.25	0.251	0.00	0.288	0.00
1.75	0.142	2.08	0.211	2.24
2.25	0.104	0.00	0.167	0.00
2.75	0.061	2.08	0.115	2.24
3.75	0.026	2.08	0.060	2.24
4.75	0.011	2.08	0.034	2.24
5.75	0.000	0.00	0.019	2.24
6.75	—	—	0.010	2.24
7.75	—	—	0.000	0.00

Data from Slade and Ralph (1974).

After density was reduced, reproduction exceeded mortality, and there was a substantial rate of population increase [$r = 0.306 \text{ individuals}/(\text{individual} \cdot \text{year})$]. The maximum life span increased to seven years, and the stable age distribution shifted slightly toward older ages (Figure 3.5a). The reproductive value showed a broader peak for three- and four-year olds (Figure 3.5b), reflecting the increased reproduction and survival of older ages.

The density reductions revealed that crowding had many effects beyond a slowing of population growth rate. Survivorship, reproduction, life span, and age structure were all sensitive to population density. The manipulations also point to a key weakness of our exponential growth model: age-specific birth and death rates change with population size!

Density dependence can be incorporated into either the mortality or the fecundity schedules for one or more age classes. Even if it limits the increase of only a single age class, density dependence can be an effective brake on total population growth, and can lead to complex population dynamics. In the remainder of this primer, we will return to simple models of populations that do not incorporate age structure. However, the biological details of migration (Chapter 4), competition (Chapter 5), predation (Chapter 6), and colonization (Chapter 7) almost certainly reflect the age and size structure within a population.

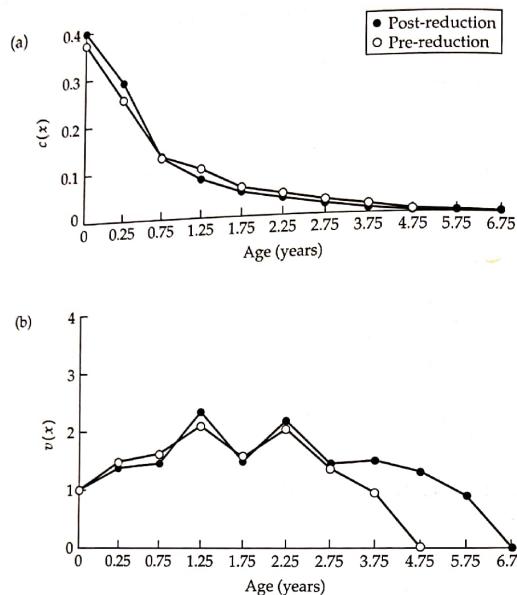


Figure 3.5 (a) Stable age distribution and (b) reproductive value distribution for Uinta ground squirrels (*Spermophilus armatus*) before and after density reduction. Data from Table 3.5.

STAGE PROJECTION MATRICES FOR TEASEL

Teasel (*Dipsacus sylvestris*) is a European perennial “weed” that is common in abandoned fields and meadows of the eastern United States. The plant has a complex life cycle that can be described with a stage-based matrix model. Most seeds fall within two meters of the adult plant, and the seeds may lie dormant for one or two years. Seeds that successfully germinate form a large-leaved rosette. The rosette phase is variable and may last for more than five years. The rosette requires cold-hardening (vernalization) before it will form a flowering stalk the following summer. Teasel flowers and sets seed only once, and then the plant dies.

Teasel was studied in eight abandoned fields in Michigan, which were sown with teasel seed at the start of the study (Werner 1977; Werner and Caswell 1977). To construct the stage-based transition matrix, individual plants were monitored in marked plots for several consecutive years. The life cycle of teasel can be divided into six stages (Caswell 1989):

1. Dormant first-year seeds
2. Dormant second-year seeds
3. Small rosettes (< 2.5 cm diameter)
4. Medium rosettes (2.5–18.9 cm diameter)
5. Large rosettes (≥ 19.0 cm diameter)
6. Flowering plants

Figure 3.6 gives the loop diagram and corresponding stage matrix for this life cycle as measured on one of the eight experimental plots. From the positive entries on the diagonals and subdiagonals, the rosettes can remain in their own size class, grow to a larger rosette size, or flower. The single entry in the first

Seed (1)	Seed (2)	Ros (s)	Ros (m)	Ros (l)	Flowering plant
0	0	0	0	0	322.380
0.966	0	0	0	0	0
0.013	0.010	0.125	0	0	3.448
0.007	0	0.125	0.238	0	30.170
0.008	0	0	0.245	0.167	0.862
0	0	0	0.023	0.750	0

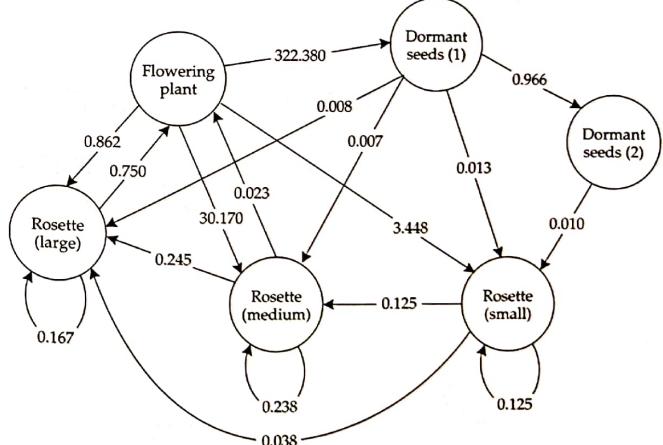


Figure 3.6 Transition matrix and loop diagram for teasel (*Dipsacus sylvestris*). Transitions are shown for dormant first-year and second-year seeds [seed (1) and seed (2)], small, medium, and large rosettes [ros (s), ros (m), ros (l)], and flowering plants. (Data from Caswell 1989.)

row of the matrix reflects the fact that only the flowering plants can produce seed. Also, notice that the diagonal element is zero for flowering plants (P_{66}), indicating that they do not survive after they flower. The population growth rate for this matrix is $\lambda = 2.3242$. This corresponds to an r of 0.8434 individuals/(individual • year), with a projected doubling time of less than 10 months.

In contrast to a simple age-classified model, relative frequencies in the stable stage distribution do not always decrease with later stages. In the stable stage distribution for teasel, there were more medium than small rosettes (Figure 3.7a). Reproductive values varied over six orders of magnitude, from a minimum for second-year dormant seeds to a maximum for flowering plants (Figure 3.7b).

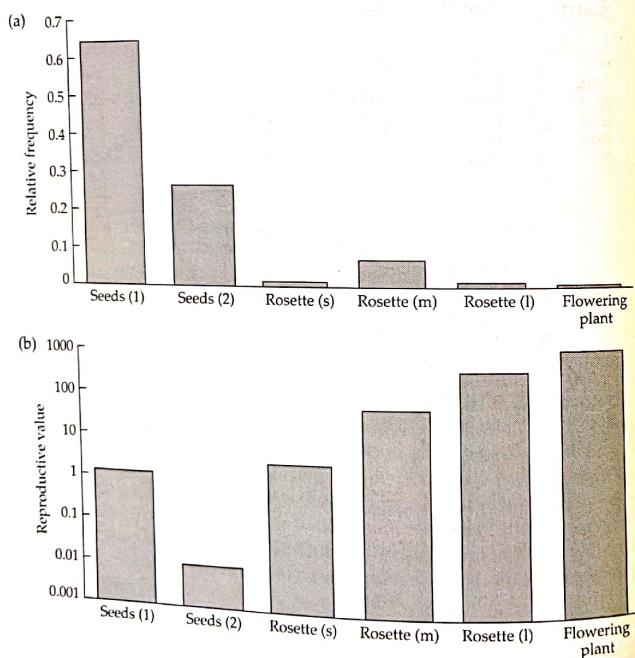


Figure 3.7 (a) Stable-stage distribution and (b) reproductive-value distribution for teasel (*Dipsacus sylvestris*). Note logarithmic scale. Derived from data in Figure 3.6.

These same data were also analyzed as an age-classified model, treating rosettes of 1–4 years as separate age classes (Werner and Caswell 1977). However, the stage-based model predicted the year of first flowering more accurately than did the age-based model. The results suggested that the size of a rosette, rather than its age, is the more important determinant of growth and survivorship for teasel.

The model results for teasel varied greatly between different fields, and population growth rates (r) ranged from -0.46 to 0.96 individuals/(individual • year). Fields with the lowest r had high levels of grass litter, which suppressed teasel seed germination. Population growth rate was also low in fields with high densities of herbaceous plants, which reduced survivorship of teasel rosettes through competition and shading. Finally, r was correlated with annual primary productivity of a field. Population growth rates were highest in the least productive fields, perhaps reflecting competition with other plants. The very high rates of increase measured for some teasel populations are unlikely to be sustained in the long run. As in the ground squirrel example, a density-dependent model may be more appropriate for forecasting population size.

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