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 $n$:

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

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

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

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 $[n(t)]$ to the next $[n(t + 1)]$.

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:

\[
P_i = \frac{l(i)}{l(i-1)} \tag{Equation 3.7}
\]

This equation is similar to the calculation of the age-specific survival probability \( \chi(x) \) (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:

\[
n_{i+1}(t+1) = P_in_i(t) \tag{Equation 3.8}
\]

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:

$$F_i = b(i)P_i$$  \hspace{1cm} \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:

$$n_1(t+1) = \sum_{i=1}^{k} F_i n_i(t)$$  \hspace{1cm} \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:

$$n_1(t+1) = F_1 n_1(t) + F_2 n_2(t) + F_3 n_3(t) + F_4 n_4(t)$$
$$n_2(t+1) = P_1 n_1(t)$$
$$n_3(t+1) = P_2 n_2(t)$$
$$n_4(t+1) = P_3 n_3(t)$$  \hspace{1cm} \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:

$$A = \begin{bmatrix} F_1 & F_2 & F_3 & F_4 \\ P_1 & 0 & 0 & 0 \\ 0 & P_2 & 0 & 0 \\ 0 & 0 & P_3 & 0 \end{bmatrix}$$  \hspace{1cm} \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,
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:

\[ n(t+1) = An(t) \]

Equation 3.11

In other words, the population vector in the next time step \([n(t+1)]\) equals the Leslie matrix \((A)\) multiplied by the current population vector \([n(t)]\). 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, \(\lambda\) is the dominant eigenvalue of the Leslie matrix. Now that we have converted our age-based life-table data for 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.

<table>
<thead>
<tr>
<th>(x)</th>
<th>(i)</th>
<th>(l(x))</th>
<th>(b(x))</th>
<th>(P_i = \frac{l(i)}{l(i-1)})</th>
<th>(F_i = \frac{b(i)}{b(i)P_i})</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>1</td>
<td>1.0</td>
<td>0</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>1</td>
<td>1</td>
<td>0.8</td>
<td>2</td>
<td>0.80</td>
<td>1.60</td>
</tr>
<tr>
<td>2</td>
<td>2</td>
<td>0.4</td>
<td>3</td>
<td>0.50</td>
<td>1.50</td>
</tr>
<tr>
<td>3</td>
<td>3</td>
<td>0.1</td>
<td>1</td>
<td>0.25</td>
<td>0.25</td>
</tr>
<tr>
<td>4</td>
<td>4</td>
<td>0</td>
<td>0</td>
<td>0.00</td>
<td>0.00</td>
</tr>
</tbody>
</table>

The resulting Leslie matrix is:

\[
A = \begin{bmatrix}
1.6 & 1.5 & 0.25 & 0 \\
0.8 & 0 & 0 & 0 \\
0 & 0.5 & 0 & 0 \\
0 & 0 & 0.25 & 0
\end{bmatrix}
\]
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):

\[
\ell(x) = \frac{e^{-rx}l(x)}{\sum_{x=0}^{k} e^{-rx}l(x)}
\]

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 \( \lambda \), 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.\(^a\)

<table>
<thead>
<tr>
<th>(x)</th>
<th>(l(x))</th>
<th>(b(x))</th>
<th>(l(x)e^{-\alpha})</th>
<th>(c(x))</th>
<th>(e^{-\alpha}/l(x))</th>
<th>(e^{-\alpha}l(y)b(y))</th>
<th>(e^{-\alpha}/l(x)b(y))</th>
<th>(v(x))</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>1.0</td>
<td>0</td>
<td>1.000</td>
<td>0.684</td>
<td>1.000</td>
<td>0.000</td>
<td>1.000</td>
<td>1.000</td>
</tr>
<tr>
<td>1</td>
<td>0.8</td>
<td>2</td>
<td>0.368</td>
<td>0.252</td>
<td>2.716</td>
<td>0.736</td>
<td>1.000</td>
<td>0.717</td>
</tr>
<tr>
<td>2</td>
<td>0.4</td>
<td>3</td>
<td>0.085</td>
<td>0.058</td>
<td>11.802</td>
<td>0.254</td>
<td>0.264</td>
<td>0.118</td>
</tr>
<tr>
<td>3</td>
<td>0.3</td>
<td>1</td>
<td>0.010</td>
<td>0.007</td>
<td>102.574</td>
<td>0.010</td>
<td>0.010</td>
<td>0.000</td>
</tr>
</tbody>
</table>

\(\alpha = 1.463\)

\(^a\)These 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.\(^b\)

<table>
<thead>
<tr>
<th>Time step (t)</th>
<th>(n_1(t))</th>
<th>(n_2(t))</th>
<th>(n_3(t))</th>
<th>(n_{total}(t))</th>
<th>(\lambda = \frac{n_{total}(t)}{n_{total}(t-1)})</th>
<th>(r = \ln(\lambda))</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>200</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>200</td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>320</td>
<td>160</td>
<td>0</td>
<td>0</td>
<td>480</td>
<td>2.4</td>
</tr>
<tr>
<td>2</td>
<td>752</td>
<td>256</td>
<td>80</td>
<td>0</td>
<td>1088</td>
<td>2.267</td>
</tr>
<tr>
<td>3</td>
<td>16,549</td>
<td>6091</td>
<td>1402</td>
<td>161</td>
<td>24,203</td>
<td>2.173</td>
</tr>
<tr>
<td>4</td>
<td>35,965</td>
<td>13,239</td>
<td>3045</td>
<td>351</td>
<td>52,600</td>
<td>2.173</td>
</tr>
<tr>
<td>5</td>
<td>78,165</td>
<td>28,772</td>
<td>6620</td>
<td>761</td>
<td>114,318</td>
<td>2.173</td>
</tr>
</tbody>
</table>

\(^b\)The 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:

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

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

$$B(t) = \int_{0}^{k} \text{(births from parents of age } x)dx$$  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 $x$ [$l(x)$]:

$$B(t) = \int_0^k B(t - x) l(x) b(x) dx$$  \hspace{1cm} \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:

$$B(t) = Ce^{rt}$$  \hspace{1cm} \text{Expression 3.12}

Substituting this back into Expression 3.12 yields:

$$Ce^{rt} = \int_0^k Ce^{r(t-x)} l(x) b(x) dx$$  \hspace{1cm} \text{Expression 3.13}

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

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

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

$$1 = \sum_{x=0}^k e^{-rx} l(x) b(x)$$  \hspace{1cm} \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):

$$v(x) = \frac{\text{number of offspring produced by individuals of age } x \text{ or older}}{\text{number of individuals of age } x}$$  \hspace{1cm} \text{Expression 3.14}

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