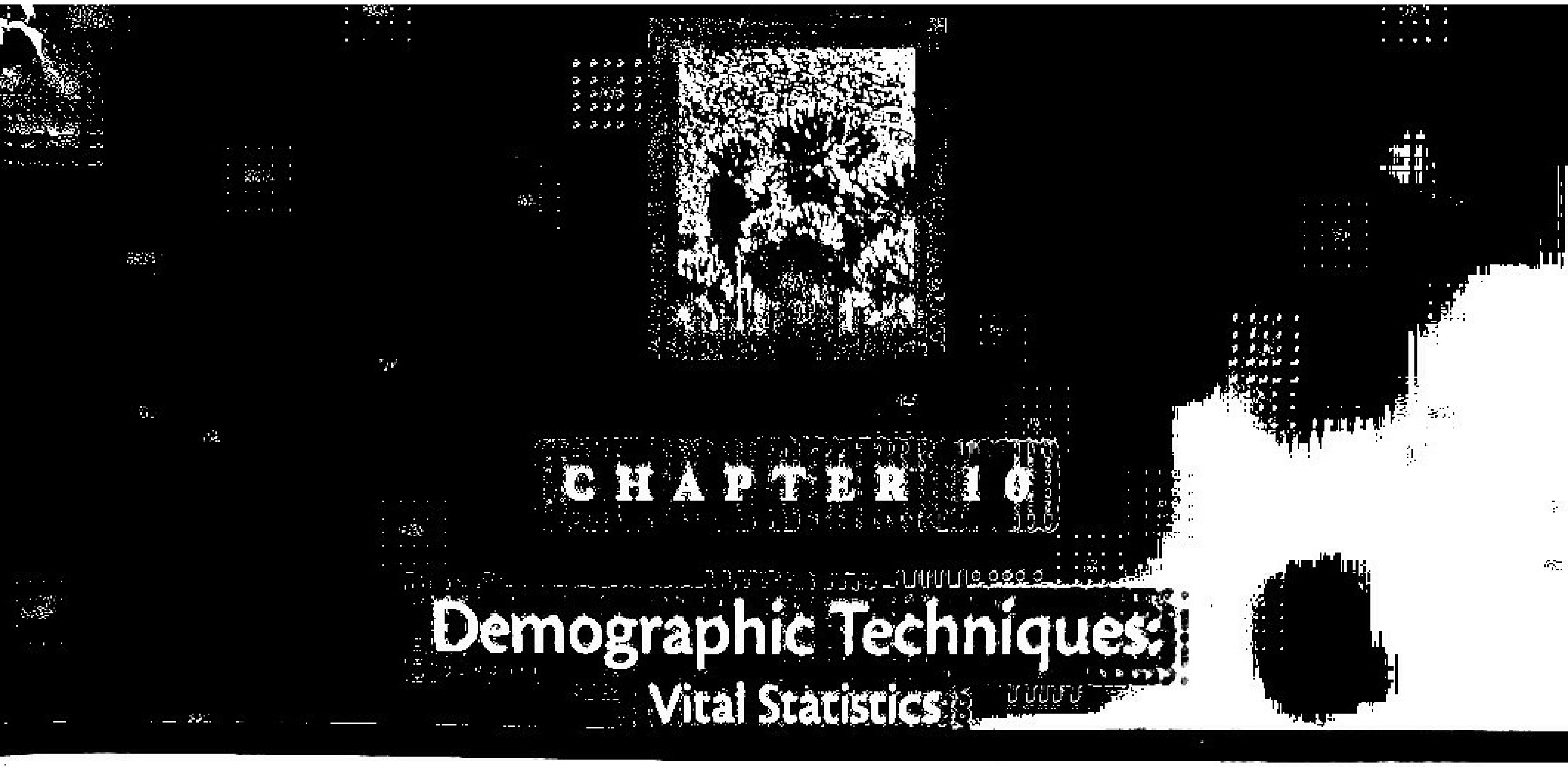

CHAPTER 10

Demographic Techniques: Vital Statistics

ONE OF THE GREAT STRENGTHS of population ecology is that it is quantitative. If the survival rate of adult bald eagles decreased 2% per year, would their populations decline? If we could increase the survival of juvenile salmon 0.5% in their first year, how many more adults would reach maturity and be available for fishermen? It is possible to answer these questions precisely with some simple mathematics. Population mathematics is not difficult, but it is sufficiently different to merit some of your attention if you wish to achieve a more precise understanding of how and why populations change. The next two chapters provide this quantitative background for population ecology.

Life Tables

Mortality is one of the four key parameters that drive population changes, as we saw in Chapter 9. We need a technique to summarize how mortality is occurring in a population. Is mortality high among juvenile organisms? Do older organisms have a higher mortality rate than younger organisms? We can answer these kinds of questions by constructing a *life table*, a convenient format for describing the mortality schedule of a population. Life tables were developed by human demographers, particularly those working for life insurance companies, which have a vested interest in knowing how long people can be expected to live. There is a correspondingly immense literature on human life tables, but few data are available on other animals or on plants.

Plant and animal populations may be composed of several types of individuals, and in any given analysis a demographer may group them together or may keep them separate. A life insurance company offers to males a policy different from the one they give to females for good demographic reasons, and thus it may be useful for some purposes to classify individuals by sex or age.

A life table is an age-specific summary of the mortality rates operating on a *cohort* of individuals. A cohort may include the entire population, or it may include only males, or only individuals born in a given year. An example of a cohort life table for song sparrows is given in Table 10.1. The columns of this life table are assigned the following symbols, which are consistently used in ecology:

x = age
n_x = number alive at age x
l_x = proportion of organisms surviving from the start of the life table to age x
d_x = number dying during the age interval x to $x + 1$
q_x = per capita rate of mortality during the age interval x to $x + 1$

To set up a life table, we must decide on age intervals in which to group the data. For humans or trees the age interval may be five years; for deer, birds, or perennial plants one year, and for annual plants or field mice one month. By making the age interval shorter, we increase the detail of the mortality picture shown by the life table.

TABLE 10.1 Cohort life table for the song sparrow on Mandarte Island, British Columbia.[a]

Age in years (x)	Observed no. of birds alive (n_x)	Proportion surviving at start of age interval x (l_x)	No. dying within age interval x to x + 1 (d_x)	Rate of mortality (q_x)
0	115	1.0	90	0.78
1	25	0.217	6	0.24
2	19	0.165	7	0.37
3	12	0.104	10	0.83
4	2	0.017	1	0.50
5	1	0.009	1	1.0
6	0	0.0	—	—

[a] Males hatched in 1976 were followed from hatching until all had died six years later. *Source:* From Smith (1988).

Note that if you are given any one of the columns of the life table, you can calculate the rest. Put another way, there is nothing "new" in each of the three columns l_x, d_x and q_x they are just different ways of summarizing one set of data. The columns are related as follows:

$$n_{x+1} = n_x - d_x \tag{10.1}$$

$$q_x = \frac{d_x}{n_x} \tag{10.2}$$

$$l_x = \frac{n_x}{n_0} \tag{10.3}$$

For example, from Table 10.1,

$$n_3 = n_2 - d_2 \qquad q_2 = \frac{d_2}{n_2} \qquad l_4 = \frac{n_4}{n_0}$$

$$= 19 - 7 = 12 \qquad = \frac{7}{19} = 0.37 \qquad = \frac{2}{115} = 0.017$$

The rate of mortality q_x is expressed as a rate for the time interval between successive census stages of the life table. For example, q_x for the song sparrows in Table 10.1 is 0.78 for the interval between egg and one year, or per year. Thus 78% of the birds are lost in the nest or during their first year of life.

The most frequently used part of the life table (see Table 10.1) is the n_x column, the number of survivors at age x. This is often expressed from a starting cohort of 1000, but some human demographers prefer a starting cohort of 100,000. Other workers prefer to plot the l_x column to show the proportion surviving. The n_x (or l_x) data are plotted as a survivorship curve; Figure 10.1 presents the survivorship curves for the human population of the United States in 1998. Note that the n_x values are plotted on a logarithmic scale.

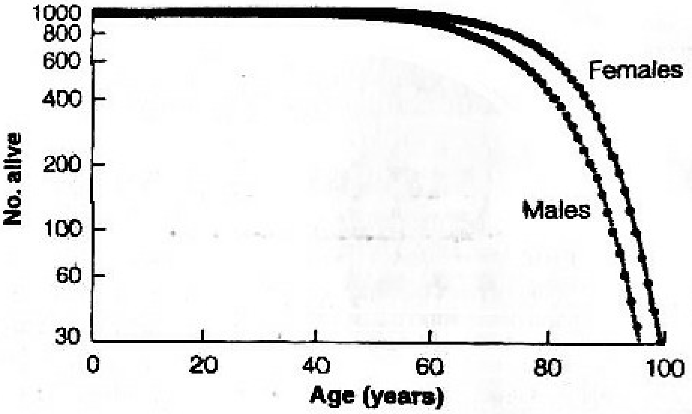

FIGURE 10.1
Survivorship curves for all males (red) and females (blue) in the United States, 1998, for a starting cohort of 1000 individuals. Life expectancy from birth for males is 73 years and for females 80 years. (Data from the U.S. National Center for Health Statistics 1999.)

Population data should be plotted this way when one is interested in per capita *rates* of change rather than absolute numerical changes (Box 10.1).

The life table was introduced to ecologists in 1921 by Raymond Pearl, one of the most important population ecologists in the United States during the first four decades of the twentieth century. Pearl (1928) described three general types of survivorship curves (Figure 10.2). Type 1 curves are characteristic of populations with low per capita mortality for most of the life span and then high losses of older organisms. The linear survivorship curve (type 2) implies a constant per capita rate of mortality independent of age. Type 3 curves indicate high per capita mortality early in life, followed by a period of much lower and relatively constant loss.

No population has a survivorship curve exactly like these idealized ones, and real curves are compos-

BOX 10.1

CALCULATION OF PER CAPITA RATES

Demographers are usually interested in per capita rates of birth and death. You can see why with a simple example. If you were told that 400 ducks had been killed in a disease outbreak, your reaction would be that this number is difficult to evaluate without knowing the size of the duck population. If you were then told that the duck population of this region was 250,000 individuals, you would be able to evaluate this mortality as a per capita rate:

$$\text{Per capita death rate} = \frac{\text{No. of deaths}}{\text{Population at risk}}$$

$$q_x = \frac{d_x}{n_x} = \frac{400}{250{,}000} = 0.0016$$

or a death rate of 0.16%, a tiny figure. Similarly, if you were told that nine marmots died in a severe storm, you would need to know that the total marmot population was 26 individuals to know that this is a high per capita mortality rate:

$$q_x = \frac{d_x}{n_x} = \frac{9}{26} = 0.346$$

and that more than one-third of the population died.

Natality rates should also be expressed as per capita rates for the same reasons.

$$\text{Per capita birth rate} = \frac{\text{No. of births}}{\text{Size of the reproductive population}}$$

Plotting population data on a logarithmic scale is a simple way to emphasize per capita rates. A numerical example shows this. If half of a population dies, we obtain:

Starting population size	*No. dying*	*Per capita death rate*	*Final population size*
1000	500	0.5	500
500	250	0.5	250
250	125	0.5	125

On a logarithmic scale, all these decreases are equal (base 10 logs):

$$\log(1000) - \log(500) = \log(500) - \log(250)$$
$$3.00 - 2.70 = 2.70 - 2.40$$

Even though *numbers* lost are greatly different, the *per capita death rates* are the same.

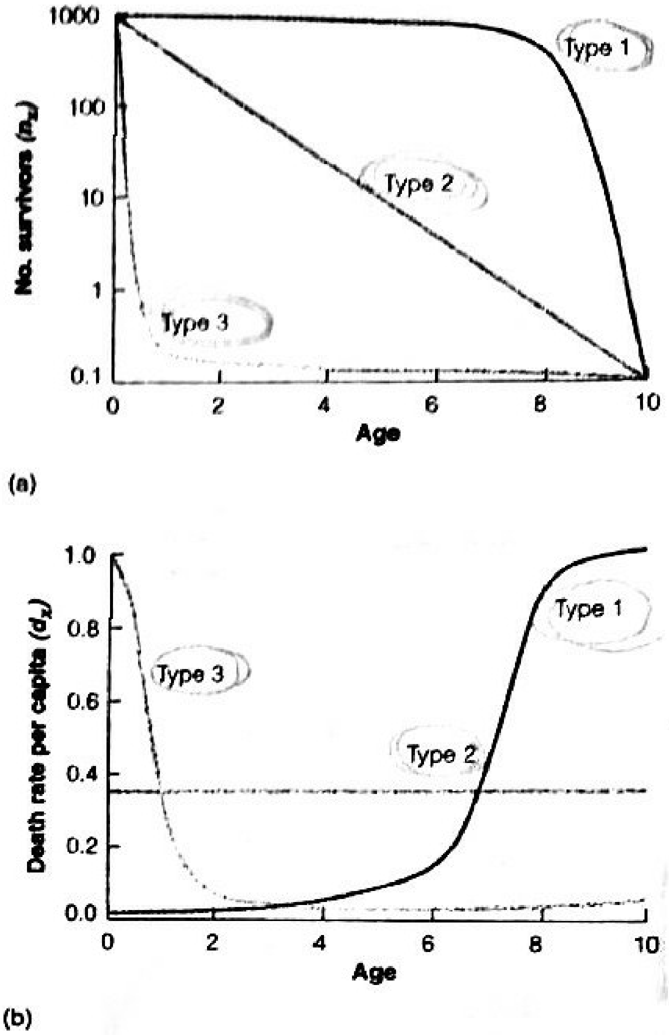

FIGURE 10.2
(a) Hypothetical survivorship curves (n_x). *(b) Mortality rate* (d_x) *curves corresponding to these hypothetical survivorship curves. Type 2 curves show constant survival rate with respect to age. Type 1 curves show increasing mortality late in life, and Type 3 curves show the highest mortality early in life. (After Pearl 1928)*

ites of the three types. In developed nations, for example, humans tend to have a type 1 survivorship curve (except for the first few days of life). Many birds have a type 2 survivorship curve, and a large number of populations would fall in the area intermediate between types 1 and 2. Often a period of high loss in the early juvenile stages alters these ideal type 1 and 2 curves. Type 3 curves occur in many fishes, marine invertebrates, and parasites.

Now that we have seen what a life table looks like, how do we get the data to construct one? The answer is: it depends, because there are two very different ways of gathering data for life tables, and they produce two different types of life tables: the cohort life table (which we have already seen in table 10.1) and the static life table. These two life tables are different in form, except under unusual circumstances, and are always quite different in meaning (Caughley 1977).

TABLE 10.2 Static life table for the Human Female Population of Canada, 1996.

Age group (yr)	*No. in each age group*	*Deaths in each age group*	*Mortality rate per 1000 persons (1000 q_x)*
0–4	955,000	1211	1.28
5–9	984,500	159	0.16
10–14	987,700	162	0.16
15–19	976,500	179	0.18
20–24	1,002,900	377	0.38
25–29	1,102,100	525	0.48
30–34	1,297,200	633	0.49
35–39	1,322,500	804	0.61
40–44	1,195,700	1031	0.86
45–49	1,074,700	1422	1.32
50–54	834,000	1899	2.28
55–59	670,700	2444	3.64
60–64	616,900	3820	6.19
65–69	593,100	5900	9.95
70–74	547,100	8642	15.80
75–79	415,100	10,789	25.99
80–84	292,700	14,226	48.60
85–90	162,300	15,739	96.97
90 and above	88,000	28,763	326.85

Source: Statistics Canada (1999).

The *static life table* (also called a stationary, time-specific, current, or vertical life table) is calculated on the basis of a cross section of a population at a specific time. Table 10.2 is a static life table composed from the census data and mortality data for human females in Canada in 1996. A cross section of the female population in 1996 provides the number of deaths (d_x) in each age group and the number of individuals in that age group. This allows us to estimate a set of mortality rates (q_x) for each age group, and the q_x values can be used to calculate a complete life table in the way outlined previously, if we assume that the population is stationary.

The *cohort life life table* (also called a generation or horizontal life table) is calculated on the basis of a cohort of organisms followed throughout life. For example, we could, in principle, get all the birth records from New York City for 1931 and trace the history of all these people throughout their lives, following those that move out of town a very tedious task.

Raymond Pearl *(1879–1940) Professor of Biometry, Johns Hopkins University*

We could then tabulate the number surviving at each age interval. Very few data like these are available for human populations[1]. This procedure would give us the survivorship curve directly, and we could calculate the other life-table functions, as previously described.

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[1] For human populations, unlike those of other animals and plants, it is posible to construct cohort life tables indirectly from mortality rate (q_x) data. To construct a cohort life table for the 1931 New York City cohort, we can obtain the mortality statistics for the 0- to 1-year-olds for 1931, the 1- to 5-year-olds for 1932–1935, the 6-to-10-year-olds for 1936–1940, and so on, and use these q_x rates to estimate the life-table functions.

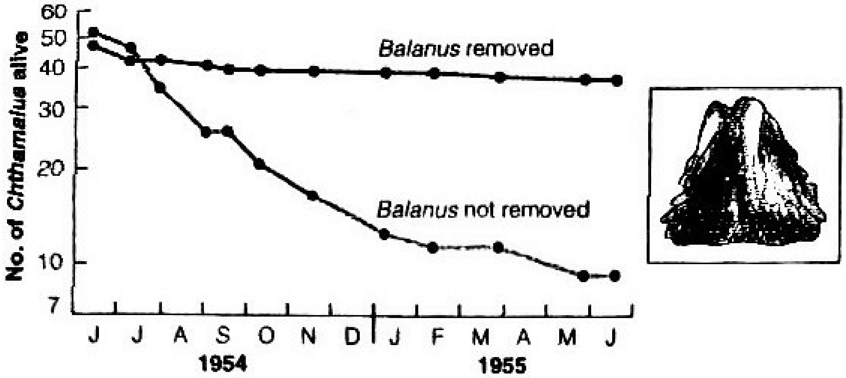

FIGURE 10.3
Survivorship curves of the barnacle Chthamalus stellatus, *which had settled naturally on the shore at Millport, Scotland, in the autumn of 1953. The survival of* Chthamalus *growing without contact with* Balanus *is compared with survival in an area with both species.* Balanus *crowds out* Chthamalus *when the two species are side by side. (Data from Connell 1961a and personal communication.)*

These two types of life table will be identical if and only *if* the environment does not change from year to year and the population is at equilibrium. But normally birth rates and death rates do vary from year to year, and consequently large differences exist between the two forms of life table. These differences can be illustrated most easily for human populations. For example, a static life table for humans born in 1900 in the United States would show what the survivorship curve would have been if the population had continued surviving at the rates observed in 1900. But of course the human population did not retain these same 1900 rates. The continual improvement in medicine and sanitation in the past 100 years has increased survival rates and life expectancy by more than 15 years, and the people born in 1900 had a cohort or generation survivorship curve unlike that of any of the years through which they lived. Static life tables assume static (stationary) populations.

Insurance companies would like to have data from cohort life tables covering the future, but these data are obviously impossible to get. Insurers are definitely not interested in cohort life tables covering the past—the life table for the 1900 cohort would be of little use for predicting mortality patterns today. So insurers use static life tables and correct them at each census. These predictions will never be completely accurate but will be close enough for their purposes.

Life tables from nonhuman populations are more difficult to come by. In general, ecologists use three types of data to construct life tables:

- *Survivorship directly observed.* The information on survival (l_x) of a large cohort born at the same time, followed at close intervals throughout its existence, is the best to have, since it generates a cohort life table directly and does not involve the assumption that the population is stable over time. A good example of data of this type is that of Connell (1961a) on the barnacle *Chthamalus stellatus* in Scotland. This barnacle settles on rocks during the autumn. Connell did several experiments in which he removed a competing barnacle, *Balanus balanoides,* from some rocks but not from others, and then about once a month counted the *Chthamalus* surviving on these defined areas (Figure 10.3). Barnacles that disappeared had certainly died; they could not emigrate.
- *Age at death observed.* Data on age at death may be used to estimate the life-table functions for a static life table. In such cases we must assume that the population size is constant over time and that the birth and death rates of each age group remain constant. A good example of this type of data comes from the work of Sinclair (1977) on the African buffalo *(Syncerus caffer)* in the Serengeti area of east Africa. On his study area Sinclair collected 584 skulls of buffalo that had died from natural causes and classified them by age and sex. The age at death was determined by examining the annular rings on the horns. Young animals were difficult to sample properly because their fragile skulls were more susceptible to damage by weather and carnivores. Sinclair estimated the losses during the first two years of life by direct observations on the herd and obtained the mortality estimates shown in Figure 10.4.
- *Age structure directly observed.* Ecological information on age structure, particularly of trees, birds, and fishes, is considerable and in some cases can be used to construct a static life table.

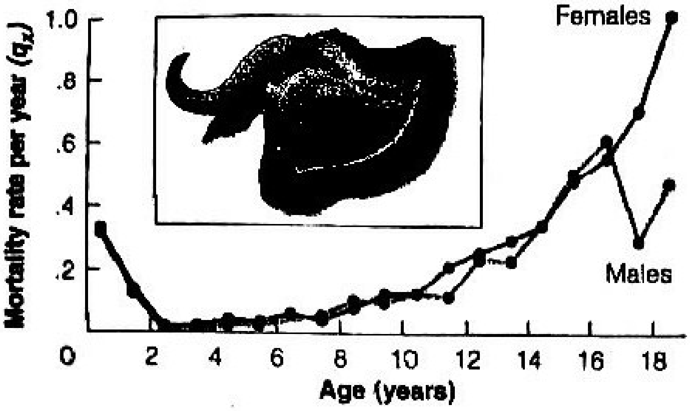

FIGURE 10.4

Mortality rate per year (q_x) for each one year age interval for the African buffalo. Age at death was determined from skulls of dead buffalo collected during a period of steady population increase. (Data from Sinclair 1977.)

In these cases, we can often determine how many individuals of each age are living in the population. For example, if we fish a lake, we can get a sample of fish and determine the age of each from annular rings on the scales. (The same type of data can be obtained from tree rings.) The difficulty is that to produce a life table from such data, we must assume a constant age distribution, something that is rare for many populations. Consequently, data of this type are not always suitable for constructing a life table.

Attempts to gather life-table data on organisms other than humans and to establish a general theory of senescence have suggested that, except for early ages when mortality is high, mortality rates (q_x) increase inexorably with age, so that for all organisms the mortality curve is roughly U-shaped, as illustrated in Figure 10.4. But this commonly accepted idea of senescence of mortality rates increasing inexorably with age, has been challenged in recent years by large-scale experiments on Mediterranean fruit flies (*Ceratitis capitata*) conducted by Carey et al. (1992) and by extensive summaries of human data by Vaupel et al. (1998). Figure 10.5 plots mortality rates for a laboratory cohort of 1.2 million Mediterranean fruit flies. The death rate for flies that survive beyond 60 days falls instead of rising, as senescence theory would predict. The implication is that our simple ideas of senescence of organisms are not correct, even for humans (Vaupel et al. 1998).

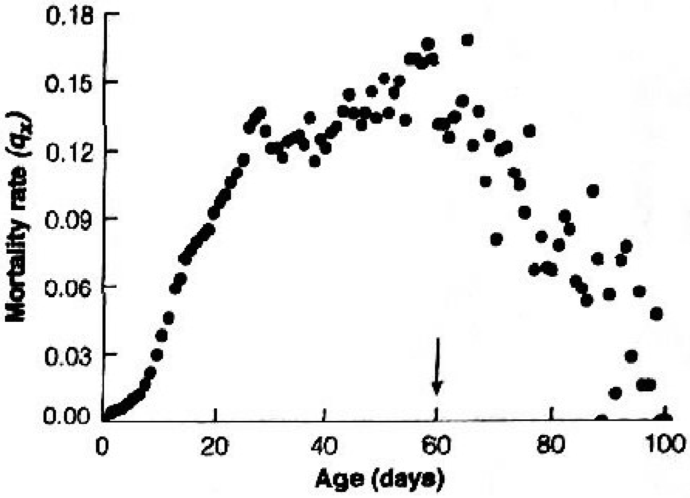

FIGURE 10.5

Age-specific mortality rates in a cohort of 1.2 million Mediterranean fruit flies (Ceratitis capitata) *raised in laboratory cages. A large initial cohort size was needed in order to insure that adequate sample sizes would be available for old flies. Note that the mortality rate does not increase continuously with age, as most models of aging have assumed, but declines after age 60 days (arrow). (Data from Carey et al. 1992.)*

Intrinsic Capacity for Increase in Numbers

A life table summarizes the mortality schedule of a population, and we have just seen several examples. We must now consider the reproductive rate of a population and techniques by which we can combine reproduction and mortality estimates to determine net population changes. Students of human populations were the first to appreciate and solve these problems. One way of combining reproduction and mortality data for populations utilizes a demographic parameter called the *intrinsic capacity for increase* derived by Alfred Lotka in 1925.

Any population in a particular environment will have a mean longevity or survival rate, a mean natality rate, and a mean growth rate or speed of development of individuals. The values of these means are determined in part by the environment and in part by the innate qualities of the organisms themselves. These qualities of an organism cannot be measured simply because they are not a constant, but by measuring their expression under specified conditions we can define for each population its *intrinsic capacity for increase* (also called the *Malthusian parameter*), a sta-

TABLE 10.3 Survivorship schedule (l_x) and fertility schedule (b_x) for women in the United States, 1996,

Age group	*Midpoint or pivotal age x*	*Proportion surviving to pivotal age l_x*	*No. female offspring per female aged x per 5-year period (b_x)*	*Product of l_x and b_x*
0–9	5.0	0.9932	0.0	0.00
10--14	12.5	0.9921	0.003	0.0030
15--19	17.5	0.9905	0.137	0.1357
20–24	22.5	0.9883	0.278	0.2747
25–29	27.5	0.9860	0.285	0.2810
30–64	32.5	0.9829	0.211	0.2074
35–39	37.5	0.9785	0.089	0.0871
40–44	42.5	0.9725	0.017	0.0165
45–49	47.5	0.9636	0.0007	0.0007
50 +	—	—	0.0	0.00

$$R_0 = \sum_{0}^{\infty} l_x b_x = 1.0061$$

Source: Statistical Abstract of the United States 1998.

tistical population characteristic that depends on environmental conditions.

Environments in nature vary continually. They are never consistently favorable or consistently unfavorable but fluctuate between these two extremes for example, from winter to summer. When conditions are favorable, numbers increase; when conditions are unfavorable, numbers decrease. It is clear that no population goes on increasing forever. Darwin (1859, Chapter 3) recognized the contrast between a high potential rate of increase and an observed approximate balance in nature. He illustrated this problem by asking why there were not more elephants, given his estimate that two elephants could give rise to 19 million elephants in 750 years.

Therefore, in nature we observe an actual rate of population change that is continually varying from positive to negative in response to changes within the population in age distribution, social structure, and genetic composition, and in response to changes in environmental factors. We can, however, ask what would happen to a population if it persisted in its current configuration of births and deaths. This abstraction is the ecologist's version of the perfect vacuum of introductory physics: we ask what would happen in terms of population increase if conditions remained unchanged for a long time in a particular environment.

An organism's innate or intrinsic capacity for increase depends on its fertility, longevity, and speed of development. For any population, these processes are integrated and measured by the natality rate and the death rate. When the natality rate exceeds the death rate, the population will increase. If we wish to estimate quantitatively the rate at which the population increases or decreases, we need to describe how both the natality rate and the death rate vary with age.

How can we express the variations of natality and mortality rates with age? We have just discussed the method of expressing survival rates as a function of age. The life table includes a table of age-specific survival rates. The portion of the life table needed to compute the capacity for increase is the l_x column, the proportion of the population surviving to age x. Similarly, the natality rate of a population is best described by an age schedule of births, seed production, egg production, or fission. This is a table that gives (for sexual species) the number of female offspring produced per female aged x to $x+1$ and is called a *fertility schedule*, or b_x function. Usually only females are counted, and the demographer typically views populations as females giving rise to more females. Table 10.3 gives the survivorship table the l_x schedule with which we are familiar and the *fertility schedule* for women in the United States in 1996. In this case, the great majority of women live through the childbearing ages. The fertility schedule gives the expected number of *female* offspring for each woman living through the five years of each age group. For example, slightly fewer than three women in 10 between the ages of 25 and 29 will, on average, have a female baby.

Given these data, we can obtain a useful statistic, the *net reproductive rate* (R_0). If a cohort of females

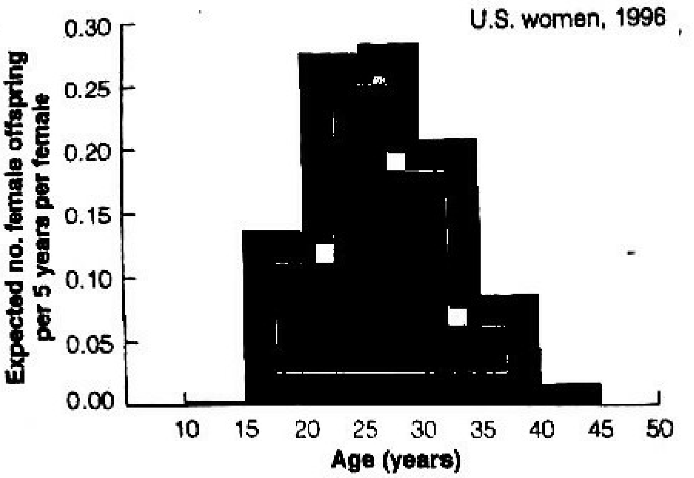

FIGURE 10.6

Expected number of female offspring per five year period for each female in the United States in 1996. Data are from the final column in Table 10.3. The area under the histogram is the net reproductive rate R_0. *(Data from the* Statistical Abstract of the United States 1998.*)*

lives its entire reproductive life at the survival and fertility rates given in Table 10.3, what will this cohort or generation leave as its female offspring? We define as the net reproductive rate as follows:

$$\text{Net reproductive rate} = R_0 \tag{10.4}$$

$$= \frac{\text{Number of daughters produced in generation } t+1}{\text{Number of daughters produced in generation } t}$$

R_0 is thus the multiplication rate per generation[2] and is obtained by multiplying together the l_x and b_x schedules and summing over all age groups, as shown in Table 10.3:

$$R_0 = \sum_{0}^{\infty} l_x b_x \tag{10.5}$$

Thus we temper the natality rate by the fraction of expected survivors to each age. If survival were 100%, R_0, would just be the sum of the b_x column. In this example (see Table 10.3), if the human population of the United States continued at these 1996 rates, it would multiply 1.006 times in each generation. If the net reproductive rate is 1.0, the population is replacing itself exactly; when the net reproductive rate is below 1.0, the population is not replacing itself; and if the rates in the example continue for a long time, the population will increase about 0.6 percent each generation in the absence of immigration or emigration. The net reproductive rate is illustrated in Figure 10.6.

Given these two schedules expressing the age-specific rates of survival and fertility, we may inquire at what rate a population subject to these rates would increase, assuming (1) that these rates remain constant and (2) that no limit is placed on population growth. Because these survival and fertility rates vary with age, the actual natality and mortality rates of the population will depend on the existing age distribution. If the whole population were over 50 years of age, it would not increase. Similarly, if all females were between 20 and 25, the rate of increase would be much higher than if they were all between 35 and 39. Before we can calculate the population's rate of increase, it would seem that we must specify (1) age-specific survival rates (l_x), (2) age-specific natality rates (b_x), and (3) age distribution.

This intuitive conclusion is not correct. Contrary to intuition, we do not need to know the age structure of the population. Lotka (1922) showed that a population that is subject to a constant schedule of natality and mortality rates will gradually approach a fixed or *stable age distribution*, whatever the initial age distribution may have been, and will then maintain this age distribution indefinitely. This theorem is one of the most important discoveries in mathematical demography. When the population has reached this stable age distribution, it will increase in numbers according to the differential equation

$$\frac{dN}{dt} = rN \tag{10.6}$$

or, as rewritten in integral form:

$$N_t = N_0 e^{rt} \tag{10.7}$$

where N_0 = number of individuals at time 0

N_t = number of individuals at time t

e = 2.71828 (a constant)

r = intrinsic capacity for increase for the particular environmental conditions

t = time

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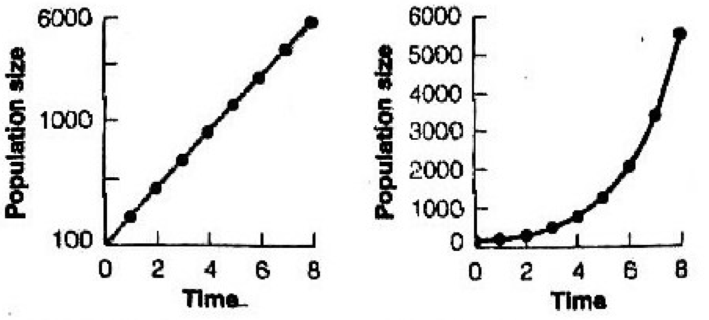
[2] A generation is defined as the mean period elapsing between the birth of parents and the birth of offspring; see page 141 and Figure 10.9.



(a) Logarithmic scale (b) Arithmetic scale

FIGURE 10.7

Geometric growth of a hypothetical population when $N_0 = 100$ *and* $r = 0.5$, *according to Equation (10.7). (a) On a logarithmic scale, geometric population growth appears as a straight line. (b) On an arithmetic scale, geometric population growth is a curve that rises more rapidly with time.*

This equation describes the curve of geometric increase in an expanding population (or geometric decrease to zero if r is negative).

A simple example illustrates this equation. Let the starting population (N_0) be 100 and let $r = 0.5$ per female per year. The successive populations would be:

Year	*Population size*
0	100
1	$(100)(e^{0.5}) = 165$
2	$(100)(e^{1.0}) = 272$
3	$(100)(e^{1.5}) = 448$
4	$(100)(e^{2.0}) = 739$
5	$(100)(e^{2.5}) = 1218$

This hypothetical population growth is plotted in Figure 10.7. Note that on a logarithmic scale the increase is linear, but on an arithmetic scale the curve swings upward at an accelerating rate.

To summarize to this point: (1) Any population subject to a fixed age schedule of natality and mortality will increase in a geometric way, and (2) this geometric increase will dictate a fixed and unchanging age distribution called the *stable age distribution*.

Let us invent a simple hypothetical organism to illustrate these points. Suppose that we have a parthenogenetic animal that lives three years and then dies. It produces two young at exactly one year of age, one young at exactly two years of age, and no young at year 3. The life table and fertility table for this hypothetical animal are thus extremely simple:

x	l_x	b_x	$l_x b_x$	$(x)(l_x)(b_x)$
0	1	0	0	0
1	1	2	2	2
2	1	1	1	2
3	1	0	0	0
4	0	-	-	-

$$R_0 = \sum_0^4 l_x b_x = 3$$

If a population of this organism starts with one individual at age 0, the population growth will be as shown in Figure 10.8 (page 142), or, in tabular form, as follows:

Year	*Number at Ages* 0	1	2	3	*Total population size*	*% Age 0 in total population*
0	1	0	0	0	1	100.0
1	2	1	0	0	3	66.7
2	5	2	1	0	8	62.50
3	12	5	2	1	20	60.00
4	29	12	5	2	48	60.42
5	70	29	12	5	116	60.34
6	169	70	29	12	280	60.36
7	408	169	70	29	676	60.36
8	985	408	169	70	1632	60.36

Note that the age distribution quickly becomes fixed or stable with about 60%at age 0, 25% at age 1, 10% at age 2, and 4 %at age 3. This demonstrates Lotka's (1922) conclusion that a population growing geometrically develops a stable age distribution.

We may also use our hypothetical animal to illustrate how the intrinsic capacity for increase r can be calculated from biological data. The data of the l_x and b_x tables are sufficient to allow the calculation of r, the intrinsic capacity for increase in numbers. To do this, we first need to calculate the net reproductive rate (R_0), explained earlier. For our hypothetical animal, $R_0 = 3.0$, which means that the population can triple its size each generation. But how long is a generation? The *mean length of a generation* (G) is the mean period elapsing between the production or "birth" of parents and the production or "birth" of offspring. This is only an approximate definition, because offspring are produced over a period of time and not all at once. The mean length of a generation is defined approximately as follows (Dublin and Lotka 1925):

$$G_c = \frac{\sum l_x b_x x}{\sum l_x b_x} = \frac{\sum l_x b_x x}{R_0} \qquad (10.8)$$

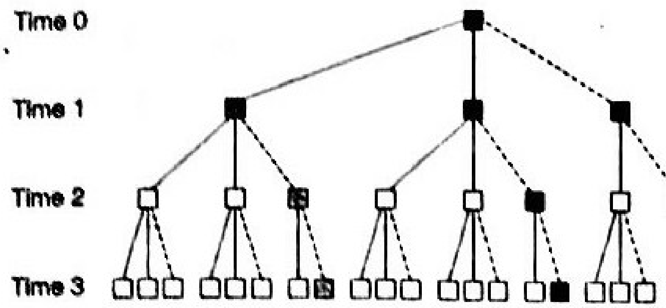


FIGURE 10.8

Population growth of a simple hypothetical organism that is parthenogenetic. Start at the top of the diagram with one green individual (each box represents one individual). At time 1 this individual gives birth to two young (yellow, red), so that there are now three individuals at time 1. At time 2 the two young individuals (red and yellow) give birth to two young each and the old green individual gives birth to one young, so at time 2 there are now eight individuals. The green individual then dies and the others reproduce, so that at time 3 there are 19 individuals. Solid lines indicate reproduction and dashed lines indicate the aging of individuals from one time to the next. Three of the individuals are color-coded to show their presence through time.

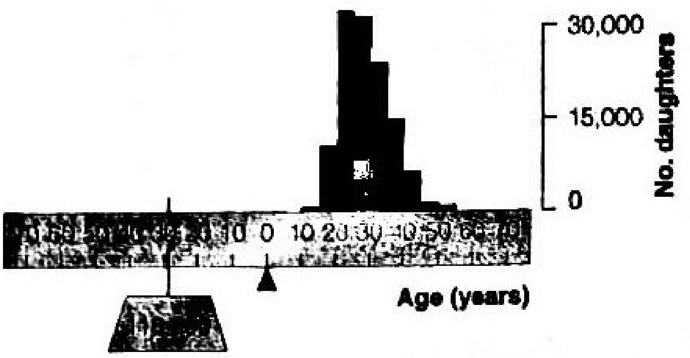


FIGURE 10.9

A mechanical balance to illustrate the idea of the mean length of one generation. Histogram of daughters from a cohort of 100,000 mothers starting life together (right side) is balanced by sum of total daughters (116,760) at exactly 28.46 years from the fulcrum. The mean length of a generation (G_c) is thus 28.46 years for these data. Data from the U.S. population of 1920, $R_0 = 1.168$.

For our model organism, $G = 4.0/3.0 = 1.33$ years. Figure 10.9 uses the metaphor of a balance to illustrate the approximate meaning of generation time for a human population. Leslie (1966) has discussed some of the difficulties of applying the concept of generation time to a continuously breeding population with overlapping generations. For organisms such as annual plants and many insects with a fixed length of life cycle, the mean length of a generation is simple to measure and to understand.

Knowing the multiplication rate per generation (R_0) and the length of a generation (G), we can now determine r directly as an instantaneous rate:

$$r = \frac{\log_e(R_0)}{G} \tag{10.9}$$

For our hypothetical organism,

$$r = \frac{\log_e(3.0)}{1.33} = 0.824 \text{ per individual per year}$$

Because the generation time G is an approximate estimate[3], this value of r is only an approximate estimate when generations overlap.

The capacity for increase is an instantaneous rate and can be converted to the more familiar finite rate[4] by the formula

$$\text{Finite rate of increase} = \lambda = e^r \tag{10.11}$$

Box 10.2 illustrates how to calculate the intrinsic capacity for increase from survivorship and fertility schedules.

It should now be clear why the intrinsic capacity for increase in numbers cannot be expressed quantitatively except for a particular environment. Any component of the environment, such as temperature, humidity, or rainfall, might affect the natality and mortality rates and hence r.

Charles Birch, working at the University of Sydney, did some of the classic early research applying these quantitative demographic techniques to insects. One illustration of the effect of the environment on the capacity for increase was developed by Birch (1953a) in his work on *Calandra oryzae*, a beetle pest that lives in stored grain. The capacity for increase in this species varied with the temperature and with the moisture content of the wheat, as shown in Figure 10.10. The practical implications of these results are that wheat should be stored where it is cool and dry to prevent losses from *C. oryzae*.

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[3] Generation time has also been defined by Caughley (1977) as:

$$G_M = \frac{\sum\left(l_x b_x x e^{-rx}\right)}{\sum\left(l_x b_x e^{-rx}\right)}$$

This will not give exactly the same value for generation time as defined in Equation (10.8); see Gregory (1997).

[4] Appendix III gives a general discussion of instantaneous and finite rates.

ESSAY 10.1

DEMOGRAPHIC PROJECTIONS AND PREDICTIONS

How much will the whooping crane population grow in the next two years? What will the AIDS epidemic do to the population of Africa between now and 2050? To answer questions such as these, we can use the demographic methods outlined in this chapter, but in doing so it is crucial that we make one subtle but important distinction: These methods can provide *projections*—that something will happen *if* conditions a and b are met—but not *predictions* that something will happen, period. (Scientists cannot predict the future; if you want a prediction, consult an astrologer or a Ouija board.) A *demographic projection* is a statement of what will happen to a population if certain assumptions are met, and demographic projections are correct only under very specific assumptions. A demographer can project population changes into the future on the assumption that, say the age-specific birth and death rates will remain constant. But in the real world the simple assumption that things will remain as they are now is rarely a correct one. Thus projections on the effects of AIDS on a population are most difficult because they require some uncertain assumptions about future death rates. Moreover, unpredictable changes such as catastrophic environmental events are especially damaging to demographic projections. No demographer can foresee mortality to half of the whooping crane population caught in an episode of severe weather.

In spite of the fact that they cannot predict the future, it is still useful for conservationists and resource managers to make projections of what will happen if specific assumptions are fulfilled. Such projections, many of which we will examine in the next several chapter, can limit our optimism and pessimism alike.

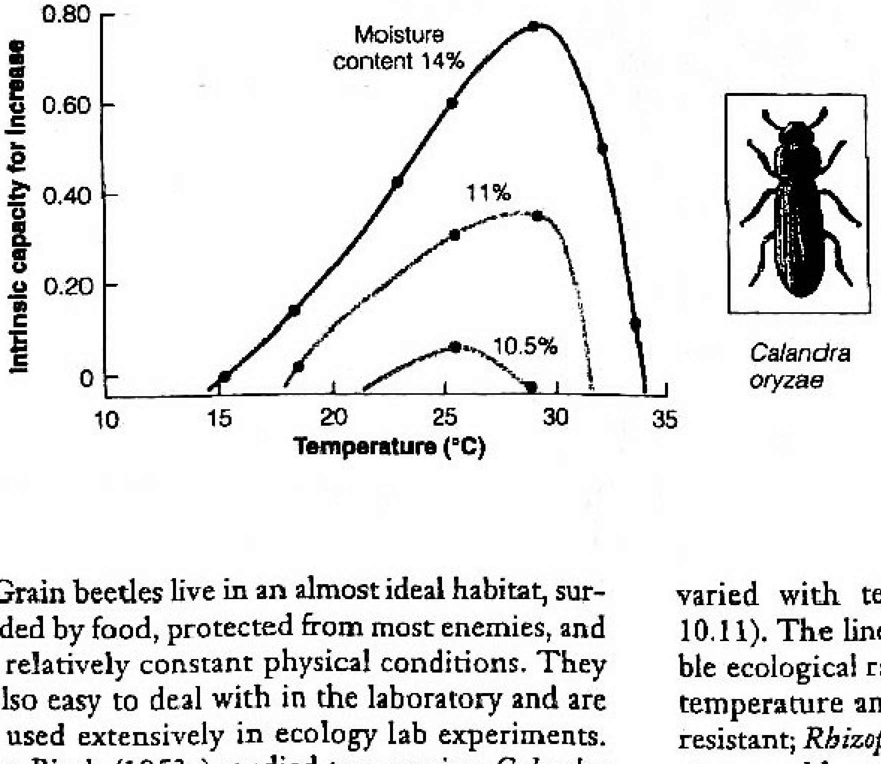


FIGURE 10.10
Intrinsic capacity for increase (r) *of the grain beetle* Calandra oryzae *living in wheat of different moisture contents and at different temperatures. The higher the moisture content of the wheat, the more rapidly these beetles can increase in numbers. (After Birch 1953a.)*

Grain beetles live in an almost ideal habitat, surrounded by food, protected from most enemies, and with relatively constant physical conditions. They are also easy to deal with in the laboratory and are thus used extensively in ecology lab experiments. When Birch (1953a) studied two species, *Calandra oryzae* (a temperate species) and *Rhizopertha dominica* (a tropical species), he found that in both species, r varied with temperature and moisture (Figure 10.11). The lines $r = 0$ mark the limits of the possible ecological range for each species with respect to temperature and moisture. *Calandra* is more cold-resistant; *Rhizopertha* can increase at higher temperatures and lower humidities. The distribution of the two species in Australia agrees with these results: *Rhizopertha* is a pest only in the warmer parts of the

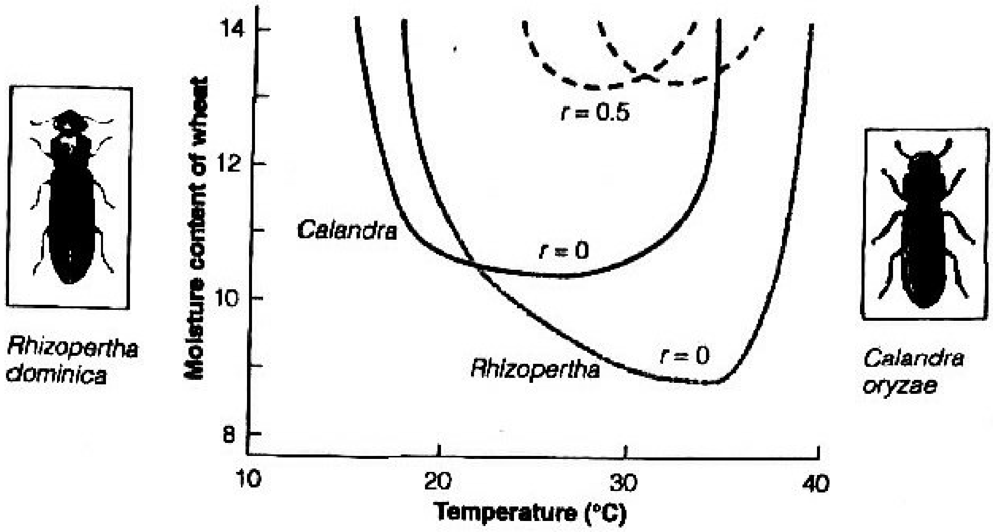


FIGURE 10.11
Intrinsic capacity for increase (r) *of the two grain beetles* Calandra oryzae *and* Rhizopertha dominica *living in wheat of different moisture content and at different temperatures. The higher the temperature and the dryer the wheat, the more* Rhizopertha *is favored. (After Birch 1953a.)*

Charles Birch *(1918–) Professor of Zoology, University of Sydney*

country and is absent from Tasmania, where *Calandra* occurs as a pest.

In general, the intrinsic capacity for increase is not correlated with the abundance of species: Species with a high *r* are not always common, and species with a low *r* are not always rare. Some species, such as the bison in North America, the elephant in central Africa, and the periodical cicadas, are (or were) quite common and yet have a low *r* value. Many parasites and other invertebrates with a high capacity for increase are nevertheless quite rare. Darwin (1859) pointed this out in *The Origin of Species*. From a conservation viewpoint species with a high *r* can recover more quickly from disturbances, and these calculations will permit us to calculate exactly how fast they might recover.

We can calculate how certain changes in the life history of a species would affect its capacity for increase in numbers. In general, three factors will increase *r*: (1) reduction in age at first reproduction, (2) increase in number of progeny in each reproductive event, and (3) increase in number of reproductive events (increased longevity). In many cases when *r* is large, the most profound effects are achieved by changing the age at first reproduction. For example, Birch (1948) calculated for the grain beetle *C. oryzae* the number of eggs needed to obtain $r = 0.76$ according to the age at first reproduction:

Age at which breeding begins (weeks)	*Total no. eggs that must be laid to produce r = 0.76*
1	15
2	32
3	67
4	141 (actual life history)
5	297
6	564

BOX 10.2

CALCULATION OF THE INTRINSIC CAPACITY FOR INCREASE FROM LOTKA'S CHARACTERISTIC EQUATION

The intrinsic capacity for increase can be determined more accurately by solving the characteristic equation, a formula derived by Lotka (1907, 1913):

$$\sum_{0}^{\infty} e^{-rx} l_x b_x = 1$$

This equation cannot be solved explicitly for r because it cannot be rearranged to have r on one side and all else on the other. By substituting trial values of r, we can solve this equation iteratively, by trial-and-error. Our hypothetical animal (see Figure 10.8) can be used as an example. For our estimate of $r = 0.824$, we get

x	$l_x b_x$	$e^{-0.824x}$	$e^{-0.824x} l_x b_x$
0	0.0	1.00	0.000
1	2.0	0.44	0.880
2	1.0	0.19	0.190
3	0.0	0.08	0.000
4	0.0	0.04	0.000

$$\sum_{0}^{\infty} e^{-rx} l_x b_x = 1.070$$

If the sum is too large (as it is here), then the estimate of $r = 0.824$ is too low. We repeat with $r = 0.85$, and after several trials we find that for this hypothetical organism, $r = 0.881$ provides

$$\sum_{0}^{\infty} e^{-rx} l_x b_x = 1.004$$

which is a close enough approximation. Carey (1993) works out another example in detail.

The intrinsic capacity for increase is an instantaneous rate (see Appendix III) and can be converted to the more familiar finite rate by the formula

$$\text{Finite rate of increase} = \lambda = e^{r} \qquad (10.11)$$

For example, if $r = 0.881$, then $\lambda = 2.413$ per individual per year in our hypothetical organism. Thus for every individual present this year 2.413 individuals will be present next year.

The earlier the peak in reproductive output, the larger the r value, as a rule. Lewontin (1965) provides an excellent example to illustrate this in *Drosophila serrata* (Figure 10.12). The Rabaul race of this fruit fly survives poorly and lays fewer eggs than the Brisbane race, but because *it* begins to reproduce at an earlier age (11.7 days compared with 16.0 days) and has a shorter generation length, its capacity for increase is equal to that of the longer-living, more fertile Brisbane race.

Demographic analyses aggregate individuals into statistical population measures such as r, the intrinsic capacity for increase. One of the difficulties of this approach is that it ignores individual variation in performance. Carey et al. (1996) developed a simple graphical technique for illustrating individual variation in demographic performance. Figure 10.13 shows the survival and lifetime reproduction for 1000 individual Mediterranean fruit fly females. By color coding the rate of egg laying and rank-ordering the individual lifetimes, these individual graphs allow us to see the detailed life history pattern of the population. The details of individual life histories can shed light on how population changes originate in the properties of individual organisms.

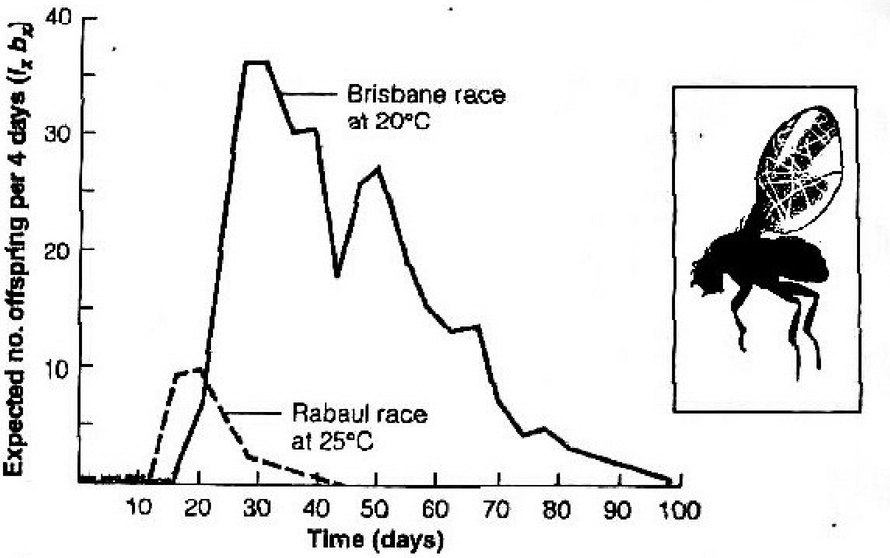
To conclude: The concept of an intrinsic capacity for increase in numbers, which we have just discussed, is an oversimplification of nature. In nature, we do not find populations with stable age distributions or with constant age-specific mortality and fertility rates. The actual rate of increase we observe in natural populations varies in more complex ways than the theoretical constant r. The importance of r lies mostly in its use as a model for comparison with the actual rates of increase we see in nature. The actual rate of increase along with its components in the life table and fertility table, can be used in the diagnosis of environmental quality because they are sensitive to environmental conditions.

Reproductive Value

We can use life tables and fertility tables to determine the contribution to the future population that an individual female will make. We call this the *reproductive value* of a female aged x (Williams 1966), and this is most easily expressed for a population that is stable in size as follows:

$$\text{Reproductive value at age } x = V_x = \sum_{t=x}^{\infty} \frac{l_t b_t}{l_x} \qquad (10.12)$$

FIGURE 10.12
Observed l_x b_x functions for two races of Drosophila serrata. *Both l_x b_x functions give the same value of the innate capacity for increase (r) because of the overriding importance of earlier reproduction and shorter generation length of the Rabaul race. Brisbane females lay an average of 546 eggs at 20°C, while Rabaul females lay only 151 eggs during their life span. (After Lewontin 1965.)*



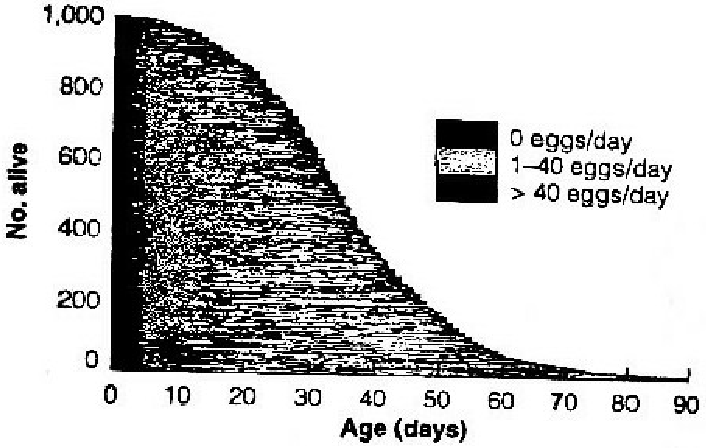


FIGURE 10.13
Graphical technique for displaying individual fertility and survival data. The life spans of 1000 Mediterranean fruit fly females is shown. Each horizontal colored line represents one individual. Individuals are ranked from the shortest life span at the top to the longest-lived individual at the bottom. (From Carey et al. 1998.)

where t and x are age and w is the age of last reproduction. Note that as defined here, reproductive value at age 0 is the same as net reproductive rate (R_0) defined on page 140.

Reproductive value can be partitioned into two components (Pianka and Parker 1975):

Reproductive value at age x = present progeny + expected future progeny

$$V_x = b_x + \sum_{t=x+1}^{w} \frac{l_t b_t}{l_x} \qquad (10.13)$$

We call the second term residual reproductive value, because it measures the number of progeny on average that will be produced in the rest of an individual's lifespan.

Reproductive value is more difficult to define if the population is not stable (Roff 1992, Stearns 1992). In this case we must discount future reproduction if population growth is occurring because the value of one progeny is less in a larger population. Figure 10.14 illustrates the change of reproductive value with age in a red deer population in Scotland. Red deer stags defend harems, and their effective breeding span is three to five years between the ages of six and 11 years. By contrast, red deer hinds start to produce calves at age 3 and breed until they are 15 years old or older. These differences in reproductive biology explain the shapes of the reproductive value curves in Figure 10.14.

Reproductive value is important in the evolution of life-history traits. Natural selection acts more strongly on age classes with high reproductive values and very weakly on age classes with low reproductive values. Predators will have a greater effect on a population if they prefer individuals of high reproductive value.

Age Distributions

We have already discussed the idea of age distribution in connection with the intrinsic capacity for increase. We noted that a population growing geometrically with constant age-specific mortality and fertility rates

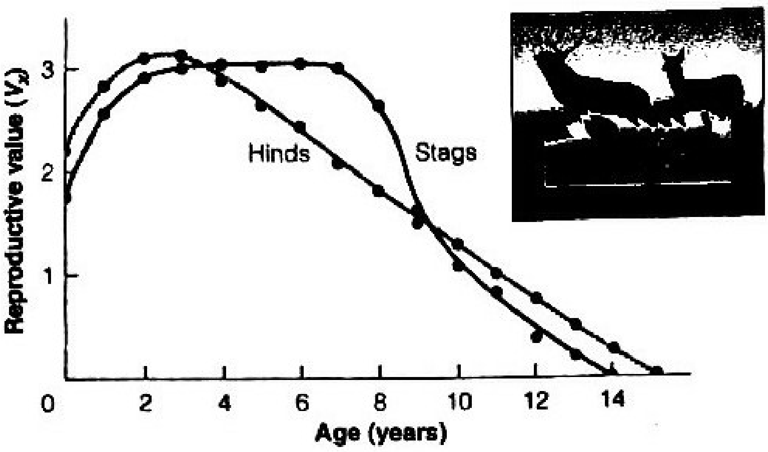


FIGURE 10.14

Reproductive value for red deer stags (males) of different ages, compared with that of hinds (females) on the island of Rhum, Scotland. Reproductive value is calculated in terms of the number of female offspring surviving to one year of age that parents of different ages can expect to produce in the future. (From Clutton-Brock et al. 1982, p. 154.)

would assume and maintain a stable age distribution. The stable age distribution can be calculated for any set of life tables and fertility tables. The stable age distribution is defined as follows:

C_x = proportion of organisms in the age category x to $x + 1$ in a population increasing geometrically

Mertz (1970) has shown that:

$$C_x = \frac{\lambda^{-x} l_x}{\sum_{i=0}^{\infty} \lambda^{-i} l_i} \qquad (10.14)$$

where $\lambda = e^r$ = finite rate of increase

l_x = survivorship function from life table

x, i = subscripts indicating age

Let us go through these calculations with our hypothetical organism:

$\lambda = e^r = e^{00881} = 2.413$

Age (x)	l_x	λ^{-x}	$\lambda^{-x} l_x$
0	1.0	1.0000	1.00001
1	1.0	0.4144	0.4144
2	1.0	0.1717	0.1717
3	1.0	0.0711	0.0711
4	0.0	0.0295	0.0000

$$\sum_{x=0}^{4} \lambda^{-x} l_x = 1.6572$$

Thus to calculate C_0, the proportion of organisms in the age category 0 to 1 in the stable age distribution, we have

$$C_x = \frac{\lambda^{-0} l_0}{\sum_{i=0}^{4} \lambda^{-i} l_i} = \frac{(1.0)(1.0)}{1.6572} = 0.6035$$

For C_1, we have

$$C_1 = \frac{\lambda^{-1} l_1}{\sum_{i=0}^{4} \lambda^{-i} l_i} = \frac{(0.4144)(1.0)}{1.6572} = 0.250$$

In a similar way,

$$C_2 = 0.104$$
$$C_3 = 0.043$$

Compare these calculated values with those obtained empirically earlier (page 141). Carey (1993) illustrates another method of calculating the stable age distribution for a set of l_x and b_x schedules.

Populations that have reached a constant size, in which the fertility rate equals the mortality rate, will also assume a fixed age distribution, called a *stationary age distribution* (or *life-table age distribution*) and will maintain this distribution. The stationary age distribution is a hypothetical one and illustrates what the age composition of the population would be at a particular set of mortality rates (q_x) if the fertility rate were exactly equal to the mortality rate. Figure 10.15 contrasts the stable and stationary age distributions for the short-tailed vole in a laboratory colony.

A constant age structure in a population is attained only if the l_x and b_x distributions are fixed and

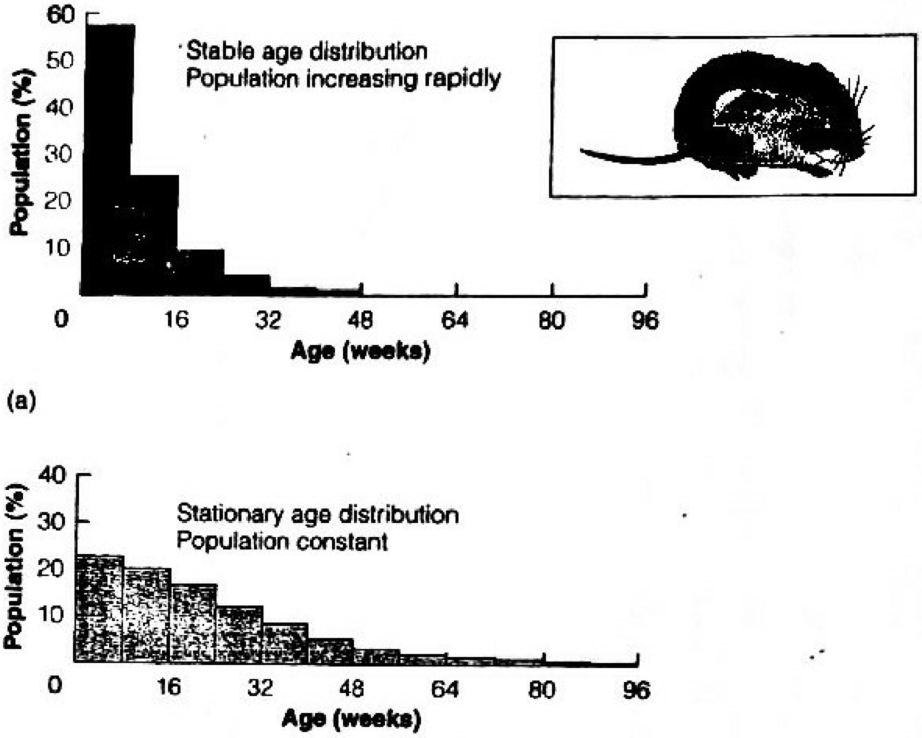
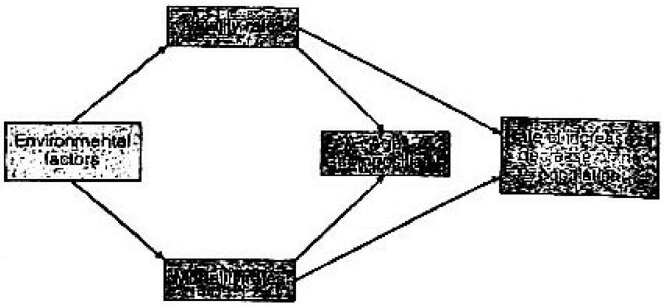


FIGURE 10.15
(a) Stable age distribution and (b) stationary age distribution for the vole Microtus agrestis *in the laboratory. The stable age distribution should be observed when populations are growing rapidly, and the stationary age distribution when populations are constant in size. (After Leslie and Ranson 1940.)*

unchanging. This typically occurs in only two situations: (1) When the age-specific fertility and mortality rates are fixed and unchanging and the population grows exponentially, the population assumes a constant age structure called the *stable age distribution;* and (2) when the fertility rate exactly equals the mortality rate and the population does not change in size over time, the population assumes a constant age structure called the *stationary age distribution* which has the same form as the l_x distribution. Under any other circumstances, the populations age structure is not a constant but the changes over time. In natural populations, the age structure is thus almost constantly changing. We rarely find a natural population that has a stable age structure because populations do not increase for long in an unlimited fashion. Nor do we often find a stationary age distribution, because populations are rarely in a stationary phase for long. We can illustrate these relationships as follows:



With proper care, information on age composition can be used to judge the status of a population. Increasing populations typically have a predominance of young organisms, whereas constant or declining populations do not (see Figure 10.15). Figure 10.16 illustrates this contrast among the human population of Kenya, which was increasing at 2.1% per year in 1995 and had an average life expectation at birth of 49 years; that of the United States, which was increasing at 0.6% per year in 1995 and had an average life expectation of about 77 years; and that of Italy, which had a zero rate of increase with an average life expectation of 78 years. The age structure of human populations has been analyzed in detail because of its economic and sociological implications (Weeks 1996). A country with a high fertility rate and a large proportion of children such as Kenya, with 46% under age 15 has a much greater demand for schools and other child services than do countries such as the United States, with 21%under age 15.

In populations of plants and animals, even more variation in age composition is apparent. In long-lived species such as trees and fishes, one may find *dominant year-classes.* Figure 10.17 illustrates this for Engelmann spruce and subalpine fir trees of the Rocky Mountains, in which some year-classes may be 100 times as numerous as others. In these situations, the age composition can change greatly from one year to

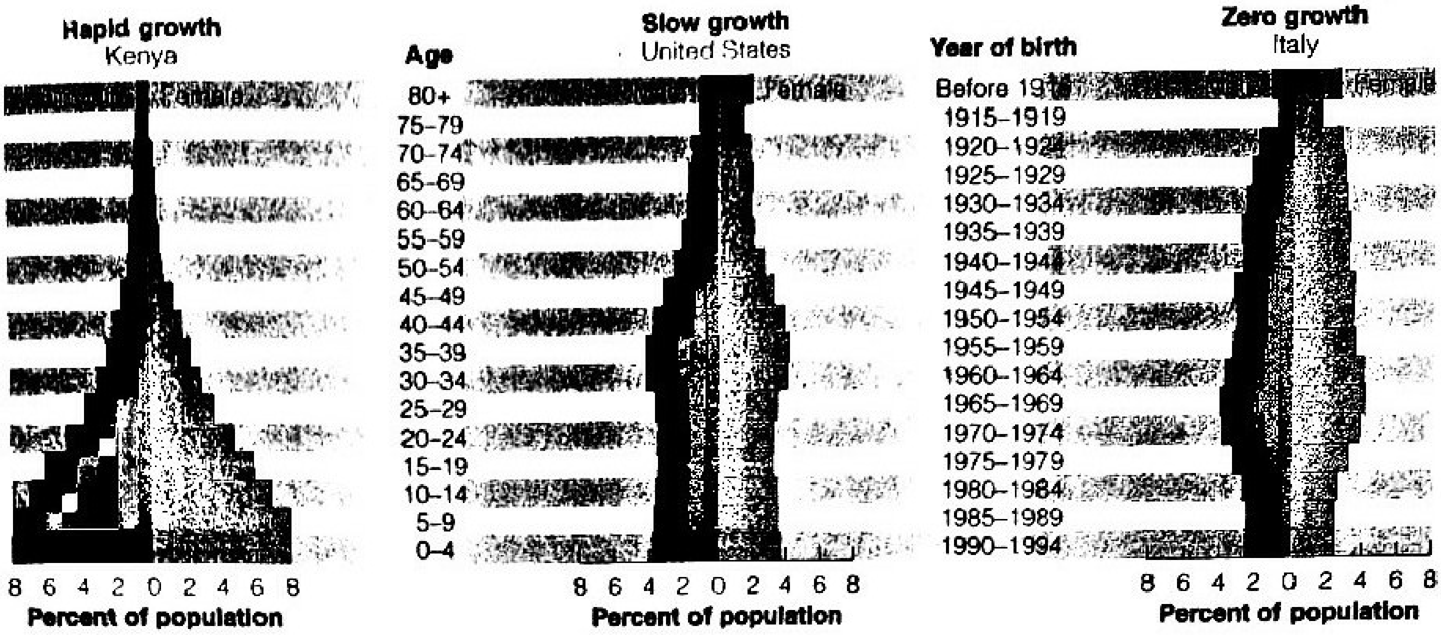


FIGURE 10.16

Age structure pyramids for the human population of Kenya (growing at 2.1% per year), the United States (growing at 0.6% per year), and Italy (zero growth) for 1995. (From McFalls 1998.)

the next. Eberhardt (1988) discusses the use of age composition information in the management of wildlife populations, and Ricker (1975, Chapter 2) discusses this problem in exploited fish populations.

Evolution of Demographic Traits

We can use the demographic techniques just described to investigate one of the most interesting questions of evolutionary ecology: Why do organisms evolve one type of life cycle rather than another? Only certain kinds of l_x and b_x schedules are permissible if a population is to avoid extinction. How does evolution act, within the framework of permissible demographic schedules, to determine the life cycle of a population?

Pacific salmon grow to adult size in the ocean and return to fresh water to spawn once and die. We may call this *big-bang reproduction*.[5] Oak trees may become mature after 10 or 20 years and drop thousands of acorns for 200 years or more. We call this *repeated reproduction*. How have these life cycles evolved? What advantage might be gained by salmon that breed more than once, or by oak trees that drop only one set of seeds and then die?

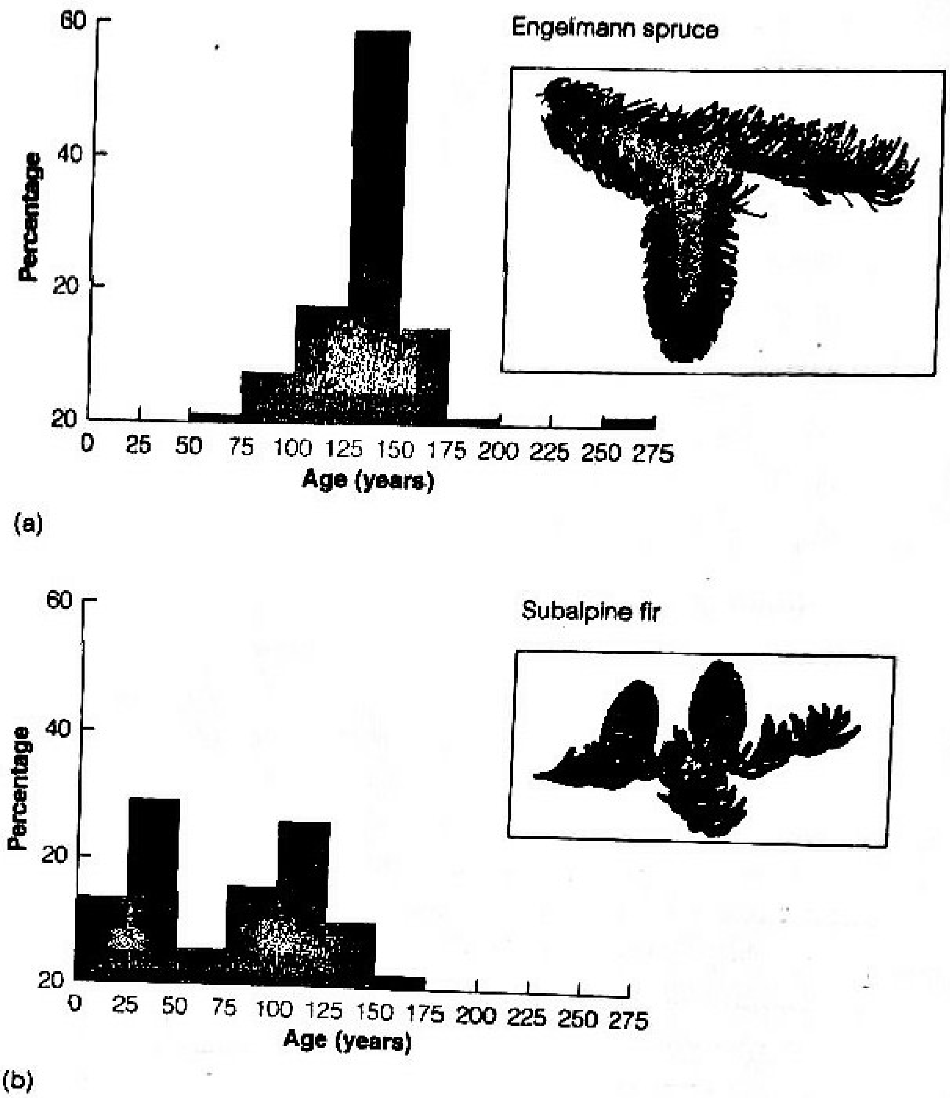
The population consequences of life cycles were first explored by Cole (1954), who asked a simple question: What effect does repeated reproduction have on the intrinsic capacity for increase (r)? Assume that we have an annual species that produces offspring at the end of the year and then dies, has a simple survivorship of 0.5 per year, and has a fertility rate of 20 offspring. The life table for this species is as follows:

Age (x)	Proportion surviving (l_x)	Fertility (b_x)	Product ($l_x b_x$)
0	1.0	0	0
1	0.5	20	10
2	0.0	-	0
			$R_0 = 10.0$

---

[5] Big-bang reproduction = semelparity, and repeated reproduction = iteroparity, for those who prefer the more classical terms derived from Greek roots.

FIGURE 10.17
Age structure of (a) Engelmann spruce and (b) subalpine fir in a forest stand at 3150 m elevation in northern Colorado. Neither of these tree species has an age distribution like those shown in Figure 10.15 for stable or stationary age distributions. (Data from Aplet et al. 1988, Table 2.)



The net reproductive rate (R_0) is 10.0, which means that the species could increase 10-fold in one generation (= 1 year). We can determine r from the characteristic equation of Lotka:

$$\text{Reproductive value at age } x = V_x = \sum_{t=x}^{\infty} \frac{l_t b_t}{l_x} \quad (10.12)$$

from which we determine that r=2.303 for the annual species with big-bang reproduction. What advantage could this species gain by continuing to live and reproduce at years 2, 3,... ∞. Let us assume the most favorable condition, no mortality after age 1 and survival to age 100. The life table now becomes the following:

Age (x)	Proportion Surviving (l_x)	Fertility (b_x)	Product ($l_x b_x$)
0	1.0	0.0	0.0
2	0.5	20	10.0
3	0.5	20	10.0
4	0.5	20	10.0
5	0.5	20	10.0
-	-	-	-
-	-	-	-
-	-	-	-
99	0.5	20.0	10.0
100	0.0	0.0	0.0

$$R_0 = \sum l_x b_x = 990.0$$

In the manner outlined above, we determine that r=2.398 for the perennial species with repeated reproduction. If we adopt repeated reproduction in our hypothetical organism, we raise the intrinsic capacity for increase only about 4%:

$$\frac{2.398}{2.303} = 1.04$$

Now let us work backward. What fertility rate at year 1 would equal the r of the perennial (2.398)? We can solve this problem algebraically (Cole 1954) or by trial and error. Suppose we increase the birth rate by one individual. The annual life table is now:

Age (x)	*Proportion Surviving (l_x)*	*Fertility (b_x)*	*Product ($l_x b_x$)*
0	1.0	0.0	0.0
1	0.5	21.0	10.5
2	0.0	-	0
			$R_0 = 10.5$

This is almost the gain achieved by repeated reproduction. If we increase the fertility rate by two individuals, we get r = 2.398, equal to the r for the perennial. This is obviously an ideal case, because we assume no mortality after age 1 in the perennial form. Cole (1954) generalized this ideal case to a surprising conclusion: For an annual species, the maximum gain in the intrinsic capacity for increase (r) that could be achieved by changing to the perennial reproductive habit would be equivalent to adding one individual to the effective litter size ($l_x b_x$ *for age 1*). Cole assumed for his ideal case perfect survival to reproductive age (Charnov and Schaffer 1973). In our hypothetical example we assumed that half of the organisms die before reaching reproductive age.

This simple model for the evolution of big-bang reproduction is unrealistic because it is a "cost-free" model: present reproduction is assumed to have no effect on future reproduction or future survival (Roff 1992, Bell 1980). Let us assume that an organism can "decide" how much of its resources it will devote to reproduction. If it uses all its resources to reproduce, it will die and thus be a big-bang reproducer. Big-bang reproduction will be favored if the greater benefits of reproduction come only at high levels of reproductive effort; conversely, if good reproductive success can be achieved at low levels of effort, organisms will be selected to be repeat reproducers. Figure 10.18 shows this trade-off between reproductive effort and reproductive success as implied in the reproductive effort model. The key demographic effect of big-bang reproduction is higher reproductive rates. Plants that reproduce only once typically produce 2-5 times as many seeds as closely related species that reproduce repeatedly (Young 1990). Repeated reproduction can also be favored when adult survival rates are high and juvenile survival is highly variable. The critical division between big-bang reproduction and repeated reproduction is set by the survival rate of the juvenile stages. If survival of juveniles is very poor or unpredictable, selection will usually favor repeated reproduction (Roff 1992). Let us look at one example to illustrate this theory.

Two species of giant rosette plants occur abundantly above treeline on Mount Kenya in Africa. *Lobelia telekii* is a big-bang reproducer that lives on

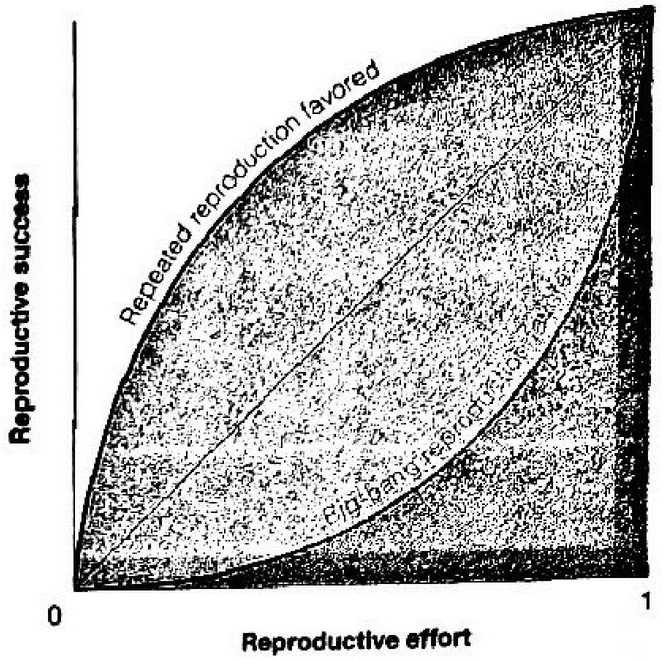


FIGURE 10.18

The reproductive effort model for the evolution of big-bang and repeated reproduction in plants and animals. The trade-off for an organism involves how much it will gain in reproductive success as it expends more and more effort on reproduction. When reproductive effort is 1, the organism breeds once and then dies (big-bang or semelparous reproduction). (Modified from Young 1990.)

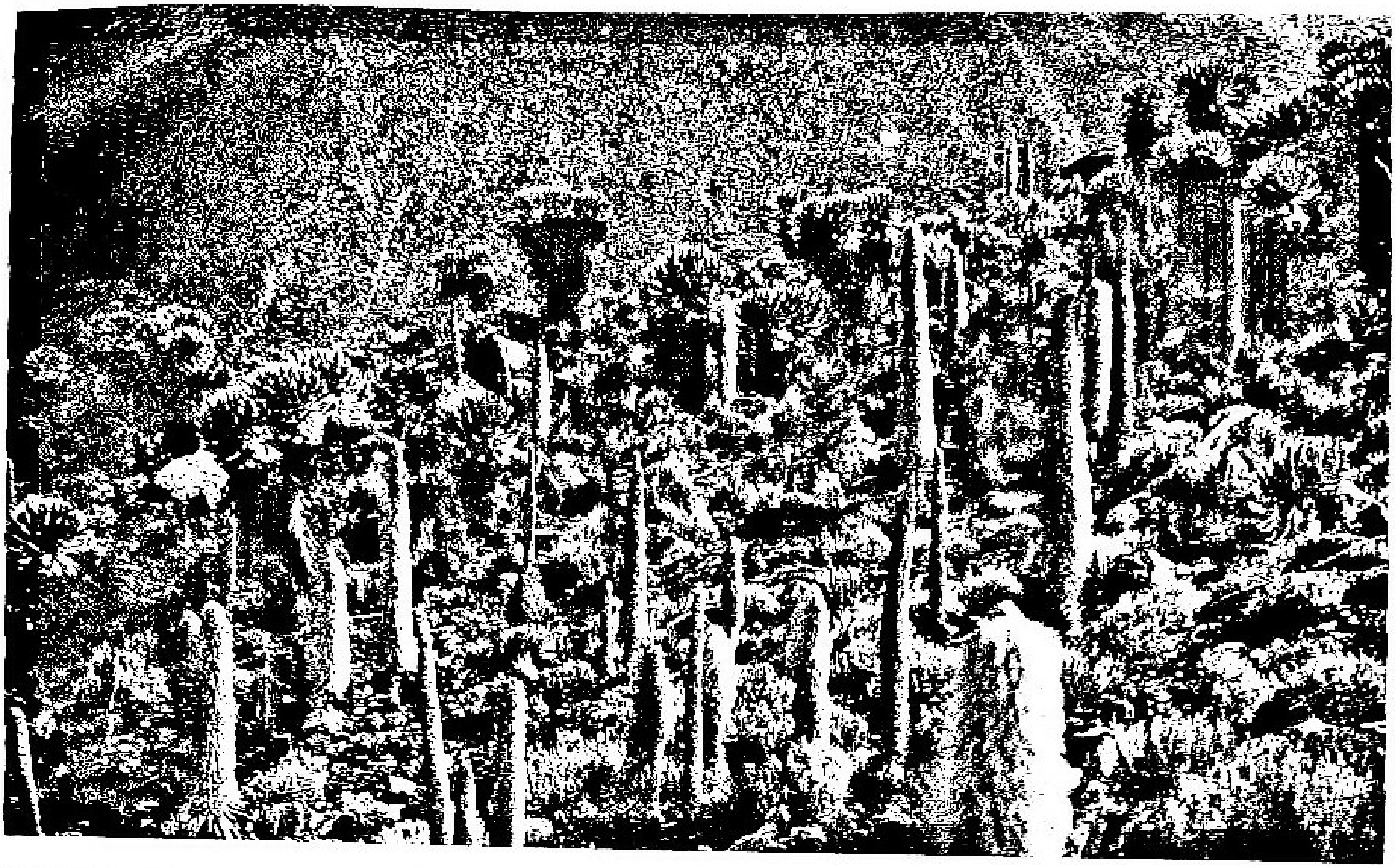


FIGURE 10.19
*Giant lobelias (*Lobelia telekii*) in the alpine zone of Mount Kenya, at 4200 m. The inflorescences of this semelparous plant are 1.5-3 m tall, and all plants die after flowering. The other giant rosette plant to the left and top of the photo is* Dendrosenecio keniodendron. *(Photo courtesy of Truman R. Young.)*

relatively dry, less productive slopes, whereas *Lobelia deckenii keniensis* is a repeated reproducer that lives in moist, more productive sites (Young 1990). Rosettes grow slowly from germination to reproductive size over 40-60 years for both species (Figure 10.19). In *Lobelia telekii* the resources of the entire plant go into reproduction, and the inflorescence may exceed 3 m in height and contain on average 500,000 seeds. After reproduction the entire plant dies. In *Lobelia deckenii keniensis* only a portion of the plant's resources goes into reproduction, and the inflorescence rarely exceeds 1 m tall and contains on average about 200,000 seeds. Big-bang reproduction in *Lobelia telekii* is favored by high mortality of adult plants in between flowering episodes the probability of future reproduction is outweighed by the greater fecundity of big-bang reproduction.

Some of the best examples of the evolution of life history strategies come from studies within a single species. Capelin are a good example because males are big-bang reproducers while females are repeated reproducers. Capelin, small (15-25g) sardine-like, pelagic fish with a circumpolar arctic distribution, form an important part of the food chain for seals, seabirds, and other fish such as cod. Males have adopted the big-bang strategy because each male can mate with several females during a spawning season and because male mortality is very high after spawning (Huse 1998). Female capelin are limited by the number of eggs they can carry, and they can improve their reproductive success only by spawning several times at yearly intervals.

Much interest in life history evolution has centered on determining the costs of reproduction. Reproductive effort at any given age can be associated with a biological *cost* and a biological *profit*. The biological cost derives from the reduction in growth or survival that occurs as a consequence of using energy to reproduce. For example, the more seeds a meadow grass (*Poa annua*) plant produces in one year, the less it grows the following year (Law 1979). Fruit fly (*Drosophila melanogaster*) females that mate often typically live shorter lives than females that mate less often (Fowler and Partridge 1989). The biological profit associated with reproduction is measured in the number of descendants left to future generations, which will be affected by the survival rate and the growth rate. The hypothetical organism must in effect ask at each age: Should I reproduce this year, or would I profit more by waiting until next year? Obviously, if the mortality rate of adults is high, it would be best to reproduce as soon as possible. But if adult mortality is low, it may pay for an organism to put its energy into growth and wait until the next year to reproduce.

Many organisms do not reproduce as soon as they are physiologically capable of doing so. The key quantity that we must measure to predict the optimal age at maturity is the *potential fecundity cost* (Bell 1980). Individuals that reproduce in a given year will often be smaller and less fecund in the following year than an individual that has previously abstained from reproduction. This is best established in poikilotherms, such as fishes, that show a reduction in growth associated with spawning. Potential fecundity costs also occur in homeotherms (Clutton-Brock et al. 1989), and the period of lactation in mammals is energetically very expensive for females (Figure 10.20). Social behavior associated with reproduction can produce great differences in the costs associated with breeding in the two sexes and thus cause differences in the optimal age at maturity for males and females. Red deer stags, for example, defend harems and attain a breeding peak after seven years of age through their fighting ability. Females mature at three years and live longer than males.

Repeated reproducers must "decide" in an evolutionary sense to increase, decrease, or hold constant their reproductive effort with age. In every case analyzed so far, reproductive effort increases with age (Sydeman et al. 1991), and this may be a general evolutionary trend in organisms.

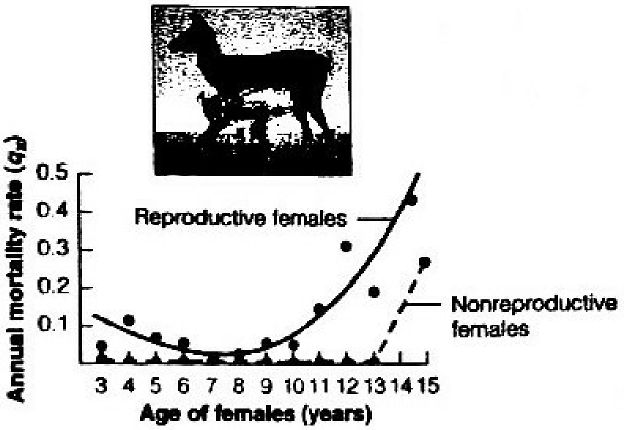


FIGURE 10.20

Cost of reproduction in female red deer on the island of Rhum in Scotland. Mortality in winter is always higher in females that reproduced during the previous summer, no matter the age of the female. (After Clutton-Brock et al. 1982.)

Why do species expend the effort to have repeated reproduction? The answer seems to be that repeated reproduction is an adaptation to something other than achieving maximum reproductive output. Repeated reproduction may be an evolutionary response to uncertain survival from zygote to adult stages (Roff 1992). The greater the uncertainty, the higher the selection for a longer reproductive life. This may involve channeling more energy into growth and maintenance, and less into reproduction. Thus we can recognize a simple scheme of possibilities:

	Long life span	*Short life span*
Steady reproductive success	?	Possible
Variable reproductive success	Possible	Not possible

We now believe that the advantage of repeated reproduction is that it spreads the risk of reproducing over a longer time period and thus acts as an adaptation that thwarts environmental fluctuations.

Summary

Population changes can be analyzed with a set of quantitative techniques first developed for human population analysis. A life table is an age-specific summary of the mortality rates operating on a population. Life tables are necessary because mortality does not fall equally on all ages, and in most species the very young and the old suffer high mortality.

A fertility schedule that summarizes reproduction with respect to age can describe the reproductive component of population increase. The intrinsic capacity for increase of a population is obtained by combining the life table and the fertility schedule for specified environmental conditions. This concept leads to an important demographic principle: A population that is subject to a constant schedule of mortality and natality rates will (1) increase in numbers geometrically at a rate equal to the capacity for increase (r), (2) assume a fixed or *stable age distribution*, and (3) maintain this age distribution indefinitely. The age distribution of a population is constant and unchanging only as long as the life table and the fertility table remain constant. Populations undergoing geometric increase reach a stable age distribution, and those showing a period of constant population size reach a *stationary age distribution*. Under other circumstances the age distribution will shift over time, which is the usual condition in natural populations.Demographic techniques are useful for comparing quantitatively the consequences of adopting an annual life cycle versus a perennial one. Very little gain in potential for population increase occurs in species that reproduce many times in each generation, and repeated reproduction seems to be an evolutionary response to conditions in which survival from zygote to adult varies unpredictably from good to poor. An organism thus "hedges its bets" by reproducing several times.

Key Concepts

1. Age-specific natality and mortality rates for any population can be summarized quantitatively in fertility schedules and in life tables.
2. The intrinsic capacity for increase (r) summarizes the natality and mortality schedules and forecasts the rate of population growth implicit in these schedules.
3. The age structure of a population is determined by these rates of natality and mortality.
4. These quantitative methods are useful for comparing the life history consequences of particular natality and mortality schedules in populations.

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