# 13 Age and stage structure

## 13.1 Introduction

In this chapter we deal with the internal workings of a population, often termed the *vital rates* or *demographic rates*, that result in a change of population size. The speed of this change is often measured as the exponential rate of increase. Any such change alerts us that the fecundity rate has changed, that the mortality rate has changed, that the age distribution has changed, or that more than one of these has changed. Each of those parameters will be considered in turn and the relationships between them explained.

We will then link the vital rates into an age-structured model to better understand how age structure influences patterns of change over time. A similar approach will be taken with populations whose demographic characteristics are better described in terms of growth stages, rather than organismal age. We demonstrate an important practical technique, elasticity analysis, which is often used by conservation biologists to evaluate the critical vital rates that may be holding back recovery of a threatened species. Finally, we use long-term demographic data from the Soay sheep population in Scotland to demonstrate how age structure, density dependence, and environmental stochasticity interact to influence population dynamics in long-lived wildlife species.

## 13.2 Demographic rates

A population's rate of increase is determined by its size, how many animals are born, and how many die during a year. Birth rate is thus an important component of population dynamics, and it can be measured in a number of ways. Of these, the most useful is fecundity rate, which we measure as the number of female live births per female per unit of time (usually one year). That figure is often broken down into age classes to give a fecundity schedule as in Table 13.1. Each value is symbolized $m_x$, female births per female in the age interval $x$ to $x + 1$.

The number of animals that die over a year is another important determinant of rate of increase, and again it can be measured in a number of ways. We measure it as the mortality rate: the number of animals that die during a unit of time (usually one year) divided by the number alive at the beginning of the time unit. As with fecundity, the rate is often given for each interval of age.

The pattern of mortality with age is summarized as a life table, which has a number of columns as in Table 13.2. The first is the age interval, labeled by the age at the beginning of the interval and symbolized $x$. The second is survivorship $l_x$, the probability at birth of surviving to age $x$. The third is mortality $d_x$, the probability at birth of dying in the age interval $x, x + 1$. The fourth, and most useful, is mortality rate $q_x$, the probability of an animal age $x$ dying before the age of $x + 1$. The fifth, age-specific survivorship $p_x$, is the probability at age $x$ that an animal will still be alive on its next birthday.

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**Table 13.1** Fecundity schedule calculated for chamois. (Source: Caughley, 1970. Reproduced with permission of De Gruyter Publishers.)

| Age in years, $x$ | Sampled number, $f_x$ | Number pregnant or lactating, $B_x$ | Female births/ female ($B_x/2f_x$), $m_x$ |
|---|---|---|---|
| 0 | – | – | 0.000 |
| 1 | 60 | 2 | 0.017 |
| 2 | 36 | 14 | 0.194 |
| 3 | 70 | 52 | 0.371 |
| 4 | 48 | 45 | 0.469 |
| 5 | 26 | 19 | 0.365 |
| 6 | 19 | 16 | 0.421 |
| 7 | 6 | 5 | 0.417 |
| >7 | 10 | 7 | 0.350 |

**Table 13.2** Construction of a partial life table.

| Age, $x$ | Survivors, $f_x$ | Survivorship, $l_x$ | Mortality, $d_x$ | Mortality rate, $q_x$ | Survival rate, $p_x$ |
|---|---|---|---|---|---|
| 0 | 1200 | 1.00 | 0.58 | 0.58 | 0.42 |
| 1 | 500 | 0.42 | 0.17 | 0.40 | 0.60 |
| 2 | 300 | 0.25 | 0.08 | 0.32 | 0.68 |
| 3 | 200 | 0.17 | - | - | - |
| … | … | … | … | … | … |

Probabilities are estimated from proportions. The probability of a bird surviving to age $x$ can be estimated, for example, by banding 1200 fledglings and recording the number still alive 1 year later, 2 years later, 3 years later, and so on. Let us say those frequencies are 500, 300, 200. Survivorship at age 0 (i.e. at birth) is $1200/1200 = 1$; by age 1 year it has dropped to $500/1200 = 0.42$; at 2 years it is $300/1200 = 0.25$; and at 3 years it is $200/1200 = 0.17$.

No further data are needed to fill in the other columns corresponding to these values of $l_x$ because each is a mathematical manipulation of the $l_x$ column. Mortality $d_x$ is calculated as $l_x - l_{x+1}$ ($1 - 0.42 = 0.58$ for $x = 0$ and $0.42 - 0.25 = 0.17$ for $x = 1$). Mortality rate $q_x$ is calculated as $(l_x - l_{x+1})/l_x$ or $d_x/l_x$ ($0.58/1 = 0.58$ for $x = 1$ and $0.17/0.42 = 0.40$ for $x = 2$). Table 13.2 shows the table fully constructed up to age 2 years. The entry for age 3 years is partial because data for age 4 years are needed to complete it. The subsequent rows would be filled in each year as the data became available.

So, constructing a life table is straightforward when the appropriate data are available. Pause for a moment to contemplate the difficulty of obtaining those data. Banding 1200 fledglings, or whatever number, poses no more than a problem in logistics. The difficulty comes in estimating what proportion of those birds are still alive at the end of the year. Nonetheless, there have been a number of direct studies of vital rates in wildlife species, based on mark–recapture methods (Lebreton *et al*. 1992; Gaillard *et al*. 2000). Approximation methods are also available, based on age structure. If one can age a sample of the living population, or alternatively establish the ages at death of a sample of deaths from that population, an approximate life table can, in some circumstances, be constructed from those age frequencies.

## 13.3 Direct estimation of life table parameters

There are basically two different ways in which life table data can be directly estimated. The first, and rarest, is to monitor the fates of all individuals in a relatively small population that is carefully studied over a long time. For example, virtually every young lion born to the population inhabiting the Serengeti plains and adjacent woodlands has been carefully monitored over the past 3 decades (Packer *et al*. 2005). The unique combination of facial spots, scars, and other features make it possible to visually recognize every individual and keep track of their fate. By collating data for each specific cohort, one can readily calculate the probability that any member born to this group survives to age $x$ (the $l_x$ series), by simply dividing the number of survivors at age $x$ by the initial group size.

Even in this ideal situation, however, there are thorny problems associated with the estimation of life table parameters. The difficult issue is that survival is like a game of chance: the outcome can vary considerably from one replicate to another (see Chapter 16). For example, a 0.5 probability of survival for an initial group of 4 individuals can lead to 0 survivors (expected 6.3% of the time), 1 survivor (expected 25% of the time), 2 survivors (expected 37.5% of the time), 3 survivors (expected 25% of the time), or even 4 survivors (expected 6.3% of the time). So the fact that 2 out of 4 individuals in a cohort survive over a given year does not conclusively demonstrate that the probability of survival really is 0.5; nor is the observation of no individuals surviving conclusive evidence against such a rate. As a result of the inherently variable nature of demographic processes, it is difficult to ascribe a particular risk of mortality with high likelihood, unless very large numbers of individuals are involved or such observations are repeated over many years.

The second way to estimate life table parameters directly is to mark a large number of individuals at time $t$ ($A_t$), then recover some of those individuals ($b_{t+1}$) in a subsequent sampling session, say a year later, to estimate the probability of survival. Marked individuals might be equipped with leg bands (as in many bird studies), ear tags (as in many studies of small mammals), or even radio transmitters (as in many studies of large mammals). If the true number of survivors is $B_{t+1}$ then the number of marked animals in the sample ($b_{t+1}$) depends on the detectability of individuals in each sample ($c$), typically under the presumption that $b_{t+1} = cB_{t+1}$. In this situation, not only is there stochastic variation to contend with but there is also sample variation associated with detectability of individuals in the population. By chance, we might detect a relatively large number of marked individuals in a subsequent sample, for reasons wholly unrelated to survival probability.

The confidence we ascribe to survival probabilities estimated using these mark–recapture techniques depends critically on sample size, probability of recapture if an animal is still alive, the mobility of marked animals and their loyalty to the site at which originally caught, the number of replicate sampling intervals, and whether or not newly marked animals have been repeatedly added to the population (Lebreton *et al*. 1992; Nichols 1992). Over the past 2 decades, there has been a revolution of sorts in the analysis of mark–recapture data, using sophisticated computer programs such as SURGE (Lebreton *et al*. 1992) and MARK (White and Burnham 1999). Many of these programs are available free of charge from their makers' Web sites. We point interested readers to the encyclopedic review of demographic methodology by Williams *et al*. (2002) for an insightful discussion of different mark–recapture approaches and their statistical analysis.

Sophisticated mark–recapture experiments aimed at estimating demographic parameters often involve comparisons among a large number of competing models (does survival vary among sexes, over time, across age groups, or between sites?). As we discuss in Chapter 15, such comparisons often require the use of information-theoretic approaches to identify the most parsimonious model by which to explain a given dataset. Recent versions of demographic analysis software, such as MARK, commonly include formal means of making choices among competing models (commonly either via AIC comparison (see Chapter 15) or likelihood-ratio testing).

## 13.4 Indirect estimation of life table parameters

If certain conditions (see the end of this section) are met, the age distribution of the living population can be used as a surrogate for the survival frequency $f_x$ of Table 13.1 to produce an approximate life table. Many of the bovids can be aged from annual growth rings on the horns; some species of deer, seals, and possums produce growth layers in the teeth; and fish form growth lines on the scales. Unbiased samples of animals from the live population or which died from natural causes yield data that may be amenable to life table analysis.

It is sometimes possible to estimate a life table from a sample of individuals taken indiscriminately from the live population. This is most often done from hunting statistics, although the reliability of such measures is often questionable, given the tendency for most hunters to select bigger or older animals. It is better to rely on catastrophic events that indiscriminately sample a cross-section of individuals in the population.

Flash floods during the autumn of 1984 killed thousands of woodland caribou from the George River herd in northern Quebec as they were migrating to their winter range. A large number of carcasses from this freak event washed up on the banks of the Caniapiscau River, where wildlife biologists working with the Quebec government retrieved them (Messier *et al*. 1988). The resulting sample of 875 female caribou aged 1 year or older was assumed to reflect the standing age composition of the living population. The frequency of newborns was estimated from calf–mother counts on the calving grounds.

If any study population is unchanging (termed "stationary"), the standing age distribution reflects survival frequencies by age. In the case of the George River caribou herd, however, a series of censuses were available showing strong evidence of exponential increase over the previous 2 decades, with $r = 0.11$ (Fig. 13.1). This introduces a bias into life table parameter estimation, because older animals were born into a much smaller population than were younger individuals. The appropriate way to cope with this bias is to transform the age-frequency data before deriving the life table. Table 13.3

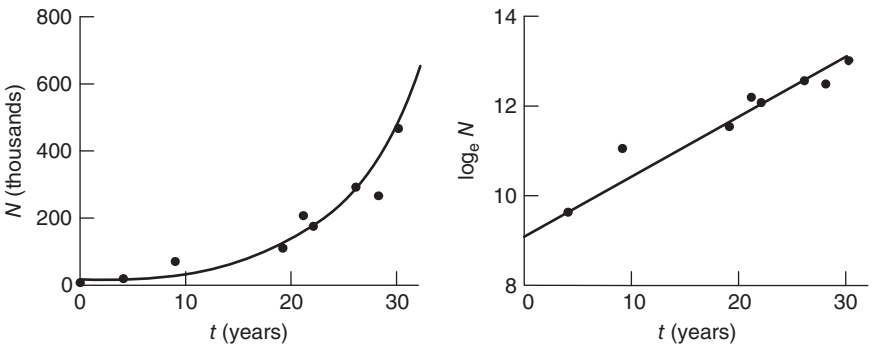


**Fig. 13.1** Exponential population growth of the George River caribou herd, as discussed in the text. (After Messier *et al*. 1988.)

**Table 13.3** Life table for female caribou in the George River herd (Source: Adapted from Messier *et al.*, 1988). Column 2 gives the original data from dead animals. Column 4 both corrects column 2 by multiplying by $e^{rx}$ and smooths out column 3.

| Age | Frequency | Corrected frequency | Smoothed frequency | $l_x$ | $d_x$ | $p_x$ | $q_x$ | $m_x$ |
|---|---|---|---|---|---|---|---|---|
| 0 | 236.1 | 236.1 | 236.1 | 1.000 | 0.286 | 0.286 | 0.714 | 0 |
| 1 | 138 | 154.0 | 168.5 | 0.714 | 0.007 | 0.010 | 0.990 | 0 |
| 2 | 156 | 194.4 | 167.0 | 0.707 | 0.017 | 0.024 | 0.976 | 0.06 |
| 3 | 113 | 157.2 | 163.0 | 0.690 | 0.027 | 0.039 | 0.961 | 0.35 |
| 4 | 94 | 145.9 | 156.6 | 0.663 | 0.037 | 0.056 | 0.944 | 0.4 |
| 5 | 83 | 143.9 | 147.9 | 0.626 | 0.044 | 0.070 | 0.930 | 0.4 |
| 6 | 65 | 125.8 | 137.3 | 0.582 | 0.053 | 0.091 | 0.909 | 0.4 |
| 7 | 63 | 136.1 | 125.0 | 0.529 | 0.057 | 0.108 | 0.892 | 0.4 |
| 8 | 57 | 137.4 | 111.4 | 0.472 | 0.063 | 0.133 | 0.867 | 0.4 |
| 9 | 40 | 107.6 | 96.6 | 0.409 | 0.065 | 0.159 | 0.841 | 0.4 |
| 10 | 24 | 72.1 | 81.2 | 0.344 | 0.067 | 0.195 | 0.805 | 0.4 |
| 11 | 18 | 60.4 | 65.4 | 0.277 | 0.067 | 0.242 | 0.758 | 0.4 |
| 12 | 12 | 44.9 | 49.5 | 0.210 | 0.066 | 0.314 | 0.686 | 0.4 |
| 13 | 7 | 29.2 | 33.9 | 0.144 | 0.064 | 0.444 | 0.556 | 0.4 |
| 14 | 1 | 4.7 | 18.8 | 0.080 | 0.061 | 0.763 | 0.238 | 0.4 |
| 15 | 4 | 20.8 | 4.4 | 0.019 | 0.019 | 1.000 | 0.000 | 0.4 |

demonstrates how to transform the age structure data, by multiplying the observed frequency at age $x$ ($f_x$) by a coefficient ($e^{rx}$) that corrects for the bias in observed age frequencies caused by population growth.

One often needs to further smooth the age-frequency data, especially when the data come from a relatively small sample of animals, in order to guarantee a continual decline in frequency with each successive age group. This is usually done by fitting a quadratic or cubic curve to the age distribution, using the values derived from the curve in place of the actual observations, as demonstrated for the George River caribou in Table 13.3. The survivorship series is then constructed by dividing each age frequency by 236, the $d_x$ series as $l_x - l_{x+1}$ and the $q_x$ series as $d_x/l_x$. If the age-frequency data had not been smoothed, there would have been instances in which the observed frequency of an older age group exceeded that in the next youngest age group, implying survival rates exceeding 100%, an obvious impossibility.

An unbiased sample of ages at death (due to natural causes), as might be obtained by a picked-up collection of skulls, may in some circumstances be treated as a multiple of the $d_x$ series. Table 13.4 gives an example from African buffalo (Sinclair 1977). Only those skulls aged 2 years or older were counted, because skulls from younger animals disintegrate quickly. These age frequencies are given in the second column of the table and total 183 skulls. The third column corrects for the missing younger frequencies: sample counts of juveniles in the field showed that the mortality rate over the first year of life was 48.5% and that 12.9% of the original cohort died in the second year. Hence, if the original cohort is taken as 1000, 485 of these would die in the first year of life and 129 in the second year. These values are tabled. They account for 614 of the original cohort, leaving 386 to die at older ages. The age frequencies of the 183 animals in the second column are thus each multiplied by 386/183 to complete the third column. The fourth column, $d_x$, is formed by dividing the $fd_x$ frequencies by 1000 so that they sum to unity. Survivorship at age 0 (i.e. birth) is then set at one and the subsequent $l_x$ values calculated by subtracting the corresponding $d_x$ from each. Mortality rates $q_x$ are calculated as before, as $q_x = d_x/l_x$.

**Table 13.4** Construction of a life table from a pick-up sample of African buffalo skulls. Uncorrected for rate of increase.

| Age, $x$ | Mortality frequency, $f_x$ | Mortality corrected, $fd_x$ | Mortality, $d_x$ | Survivorship, $l_x$ | Mortality rate, $q_x$ |
|---|---|---|---|---|---|
| 0 | - | 485 | 0.485 | 1.000 | 0.485 |
| 1 | - | 129 | 0.129 | 0.515 | 0.250 |
| 2 | 2 | 4 | 0.004 | 0.387 | 0.010 |
| 3 | 5 | 11 | 0.011 | 0.383 | 0.029 |
| 4 | 5 | 11 | 0.011 | 0.372 | 0.030 |
| 5 | 6 | 13 | 0.013 | 0.361 | 0.036 |
| 6 | 18 | 38 | 0.038 | 0.348 | 0.109 |
| 7 | 17 | 36 | 0.036 | 0.310 | 0.116 |
| 8 | 20 | 42 | 0.042 | 0.274 | 0.153 |
| 9 | 17 | 36 | 0.036 | 0.232 | 0.155 |
| 10 | 15 | 32 | 0.032 | 0.196 | 0.163 |
| 11 | 16 | 34 | 0.034 | 0.164 | 0.207 |
| 12 | 18 | 38 | 0.038 | 0.130 | 0.292 |
| 13 | 15 | 32 | 0.032 | 0.092 | 0.348 |
| 14 | 14 | 29 | 0.029 | 0.060 | 0.483 |
| 15 | 8 | 17 | 0.017 | 0.031 | 0.548 |
| 16 | 5 | 10 | 0.010 | 0.014 | 0.714 |
| 17 | 1 | 2 | 0.002 | 0.004 | 0.500 |
| 18 | 0 | 0 | 0.000 | 0.002 | 0.000 |
| 19 | 1 | 2 | 0.002 | 0.002 | 1.000 |
| *Total* | 183 | 1001 | 1.001 | | |

The reliability of any life table developed indirectly from a sample of either the live population or animals that died of natural causes depends on how closely the data meet the underlying assumptions of the analysis:

**1** The sample is an unbiased representation of the living age distribution in the first case or of the true frequency of ages at death in the second. The exercise would have to control the usual biases implicit in hunting activities if the sample of the living age distribution were obtained by shooting. One would be unlikely to use a sample obtained by sporting hunters, for example. The first age class is usually underestimated in a picked-up sample of ages at death because the skulls of young animals disintegrate much faster than do those of adults, significantly biasing the table.
**2** Age-specific fecundity and mortality must have remained essentially unchanged for a couple of generations.
**3** Whether the sample is of the living population or of ages at death, the population from which it came must have a rate of increase very close to zero, or else the data must be transformed to accommodate the observed rate of population change over the past two generations. Major fluctuations in recent rates of population growth invalidate virtually all such indirect methods. This can limit the usefulness of such exercises in wildlife management.

## 13.5 Relationships among parameters

We restrict the following discussion to females for simplicity, but the points made apply equally to the male segment of the population. Remember that $l_x$ is survivorship to age $x$, $m_x$ is production of daughters per female at age $x$, and $r$ is the exponential rate at which the population increases. These parameters are all interrelated according to the following formula (commonly termed Euler's equation):

$$\Sigma l_x m_x e^{-rx} = 1$$

If the survivorship and fecundity schedules hold constant, the population's age distribution will converge to the constant form of:

$$S_x = l_x e^{-rx}$$

which is called the *stable age distribution*. $S_x$ is the number of females in a particular age class divided by the number of females in the first age class. The basic equation may thus be written $\Sigma S_x m_x = 1$. In the special case of rate of increase being zero, the stable age distribution, now called the *stationary age distribution*, is $S_x = l_x$ by virtue of $e^{-0x} = 1$. This is the justification for using such an age distribution to construct a life table. The *stationary age distribution* is the special case of the stable age distribution that results when $r = 0$. It has been argued that, since fecundity and mortality schedules seldom remain constant for long, the stable age distribution is little more than a mathematical abstraction, albeit a useful one. Although the stable distribution can be attained fairly quickly (roughly two generations) after mortality and fecundity patterns stabilize, most wildlife species that have been adequately studied have mortality and fecundity schedules that fluctuate, sometimes substantially, from year to year.

## 13.6 Age-specific population models

All wildlife populations have individuals of different ages. The vital rates (i.e. birth rates and probabilities of survival and mortality) often vary with age. Hence, a population composed of old individuals might well exhibit a different potential for growth than does a younger population. Assessing these kinds of process requires an age-specific model of population growth (Caswell 2001).

The standard technique is to use a Leslie matrix model, named in honor of the British ecologist who pioneered this approach (Leslie 1945, 1948). This involves multiplying age-specific population densities by a transition matrix ($A$). The top row of $A$ reflects the probability of survival $p$ from the previous age class multiplied by fecundity $m$ at age $x$. The matrix elements along the subdiagonal and in the lower right-hand corner reflect the age-specific survival probabilities, $p_0, p_1$ , and $p_2$.

In order to run the Leslie matrix model, we need to specify three other vectors: the initial age distribution of the population $n$, the age-specific rates of survival $p$, and the age-specific fecundity rates $m$. The demographic parameters we are using in this case come from the Serengeti population of cheetahs, based on a study of individually recognizable individuals that spans 3 decades (Kelly and Durant 2000; Durant *et al.* 2004). Typical of most long-lived organisms, survival rates of immature cheetahs (68%) are lower than those of adults (85%).

Provided that we have an initial age distribution, we can apply the Leslie matrix to estimate the abundance of individuals in each age group in subsequent years. This is done by multiplying the matrix $A$ by the age vector $n$. A reminder of matrix algebra may be helpful here. Provided that an age vector has the same number of rows as the matrix has rows and columns, we can multiply them in the following manner. The first subscript refers to the row and the second to the column:

$$n_{0,t+1} = A_{0,0}n_{0,t} + A_{0,1}n_{1,t} + A_{0,2}n_{2,t}$$
$$n_{1,t+1} = A_{1,0}n_{0,t} + A_{1,1}n_{1,t} + A_{1,2}n_{2,t}$$
$$n_{2,t+1} = A_{2,0}n_{0,t} + A_{2,1}n_{1,t} + A_{2,2}n_{2,t}$$

This would obviously be rather cumbersome to calculate by hand for very long, especially for a species with more age groups. Fortunately, there is a simple way to automate

the procedure, using matrix operations:

$$n^{\langle t+1\rangle} = A \cdot n^{\langle t\rangle}$$

The "<>" notation used here refers to the age-specific abundance in year $t$. Hence, $n^{<2>}$ stands for the vector of age-specific abundances in year 2.

The age-specific totals predicted by the model are shown in the matrix termed "$n$." The first column of the matrix is the initial density of individuals in each age group, with newborns on the top row and old individuals on the bottom. Each column thereafter represents densities in successively later years.

$$n = \begin{pmatrix} 30 & 1.36 & 1.77 & 7.77 & 6.91 & 6.27 & 6.97 & 7.39 & 7.61 & 7.95 & 8.32 & 8.69 \\ 2 & 20.37 & 0.92 & 1.2 & 5.28 & 4.69 & 4.26 & 4.73 & 5.02 & 5.17 & 5.4 & 5.65 \\ 3 & 3.92 & 17.17 & 15.28 & 13.85 & 15.4 & 16.33 & 16.82 & 17.56 & 18.39 & 19.2 & 20.05 \end{pmatrix}$$

Model predictions of total population density, obtained by summing the densities of all age groups present at any point in time $\left(N_t = \sum n_{x,t}\right)$, are shown in Fig. 13.2.

After an initial period of adjustment, the population settles into a pattern of geometric (i.e. exponential) population growth, whose finite rate of increase depends on the integrated combination of age-specific parameters.

Each age-specific proportion $W_{x,t}$ is given by:

$$W_{x,t} = \frac{n_{x,t}}{N_t}$$

As the population settles into a geometrical growth pattern, the proportions of each age class in the population ($W_{x,t}$) converge on a stable age distribution, illustrated in Fig. 13.3. The time it takes for the age structure to stabilize is typically 2–3 generations, where generation time is the average time that elapses between the birth of a female and that of her daughters.

So, over time, we can be sure of two things: (i) the population will eventually grow geometrically and (ii) once this happens, the proportions of individuals in each age group will also become constant. The findings of geometric increase in $N$ and stable age

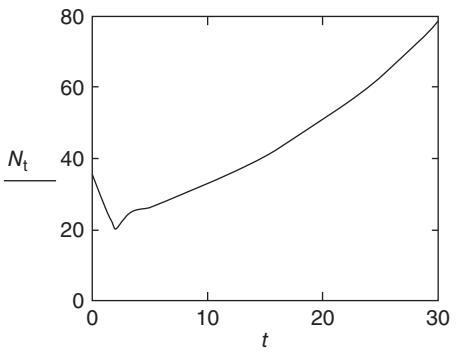


**Fig. 13.2** Predicted pattern of population change over time for the Leslie matrix model example discussed in the text.

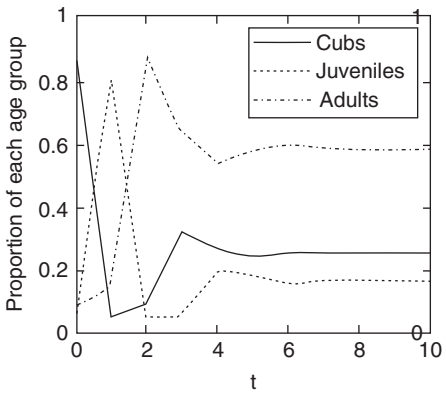


**Fig. 13.3** Predicted age distribution over time for the Leslie matrix model example discussed in the text. After 6 years, the proportions of each age group have stabilized.

distribution imply that the following mathematical statements are equivalent: $N_{t+1} = \lambda N_t$ and $n^{<t+1>} = An^{<t>}$, where $N$ and $\lambda$ are *scalars* (i.e. single, countable numbers) and $A$ and $n$ are *matrices* or *vectors*. In other words, a simple model of geometric increase ($N_{t+1} = \lambda N_t$) yields the same results as the Leslie matrix model ($n^{<t+1>} = An^{<t>}$). This means that we can estimate $\lambda$ (the finite annual rate of increase) from the transition matrix $A$, by finding something called the *dominant (largest) eigenvalue* of the transition matrix. The largest of the eigenvalues (1.04) is the finite rate of population increase ($\lambda$) once the population has reached a stable age distribution:

$$eigenvals(A) = \begin{pmatrix} -0.1 + 0.44i \\ -0.1 - 0.44i \\ 1.04 \end{pmatrix}$$

Hence, after the initial period of uncertainty, the total population will increase by 4% per year (because $\lambda = 1.04$).

Just as there is a simple means of estimating the eventual rate of population growth (dominant eigenvalue), there is an equally simple way of predicting the eventual proportion of individuals in each age group – the stable age distribution $S$ alluded to earlier. We calculate the so-called "right eigenvector" corresponding to the "dominant eigenvalue" of the transition matrix $A$:

$$S_{raw} = eigenvec(A, 1.04) \qquad S_{raw} = \begin{pmatrix} 0.38 \\ 0.25 \\ 0.89 \end{pmatrix}$$

It is easier to interpret these values if we transform them into proportions:

$$S = \frac{S_{raw}}{\Sigma_i S_{raw_i}} \qquad S = \begin{pmatrix} 0.25 \\ 0.16 \\ 0.58 \end{pmatrix}$$

In other words, once the rate of growth has stabilized, newborns will comprise 25%, 1-year-olds 16%, and adults 58% of the population.

The discussion of right eigenvectors and eigenvalues can be unnerving for many biologists, even for hardened professionals, but do not worry too much. Although the

terms sound mysterious, the meanings of "eigenvalue" and "eigenvector" are actually fairly simple. Once a population has converged on its stable age distribution, thereafter every year the total population $N$ increases by a multiplicative factor $\lambda$ (the dominant eigenvalue), meaning that each age group in the population also increases year-to-year by the same factor. So, an eigenvector is just a string of numbers (the stable age distribution) that produces exactly the same outcome when multiplied by the constant $\lambda$ as by the transition matrix $A$. Fortunately, we can use this string of numbers in a very practical way, because it tells us the relative proportion of individuals we can expect eventually to see over time in each age category.

## 13.7 Elasticity of matrix models

The largest eigenvalue of the cheetah transition matrix equals 1.04, implying that the population is just able to sustain itself (a value of 1.0 is required for sustainability, i.e. a stationary population). Age- or stage-specific models also offer useful insights into possible remedies to counteract such population declines. By modifying vital rates, one can interpret the effectiveness of possible conservation actions that might be taken. In the case of cheetahs, for example, it might be possible to protect cubs or alternatively to improve adult survival. How can we evaluate these options?

There is an easy (but not very exact) way to do this, by substituting different values for each parameter in the transition matrix and seeing which one has the biggest effect. You should do so for yourself, to determine which parameter is most conducive to improving the growth rate $\lambda$. A more elegant answer can be obtained by using calculus to determine how *sensitive* $\lambda$ is to a proportionate change in each parameter $A_{ij}$ in the transition matrix, where $i$ refers to row and $j$ to column. This is termed by ecologists the *elasticity* of $\lambda$, and the derivation is presented in Box 13.1 (based on Caswell 1978; de Kroon *et al*. 1986). It is calculated in the following manner:

$$E_{i,j} = \frac{A_{i,j}}{\lambda} \cdot \left( \frac{V_i \cdot S_j}{V \cdot S} \right)$$

**Box 13.1** Deriving the elasticity of matrix models (Caswell 1978).

For small changes in $\lambda$ as a function of small changes in any element of the transition matrix ($A_{ij}$), elasticity is defined in the follow manner:

$$\text{elasticity} = \frac{d}{dlnA_{ij}} \ln \lambda$$

$$\frac{d}{dlnA_{ij}} \ln \lambda = \frac{A_{ij}}{\lambda} \cdot \frac{d}{dA_{ij}} \lambda$$

and:

$$\frac{A_{ij}}{\lambda} \cdot \left( \frac{d}{dA_{ij}} \lambda \right) = \frac{A_{ij}}{\lambda} \cdot \left( \frac{V_i \cdot W_j}{V \cdot W} \right)$$

So:

$$\text{elasticity} = \frac{A_{ij}}{\lambda} \cdot \left( \frac{V_i \cdot W_j}{V \cdot W} \right)$$

where $V \cdot W$ in the denominator refers to the scalar or dot product obtained by multiplying together the column vector representing the stable stage distribution $W$ and the row vector of reproductive values $V$.

where $W$ is the vector corresponding to the stable age distribution and $V$ is the *vector of reproductive values*. It is the left eigenvector (as opposed to the stable age distribution, which is the right eigenvector) that corresponds to the dominant eigenvalue $\lambda$. The left eigenvector is a string of numbers that satisfies the following equality:

$$V^T \cdot A = \lambda \cdot V^T$$

where the $T$ means that we are transposing the vector, so that it is now a row (rather than a column) vector. Stage-specific reproductive values for Serengeti cheetahs are calculated as follows:

$$V_{raw} = eigenvec(A^T, 1.040) \qquad V_{raw} = \begin{pmatrix} 0.33 \\ 0.51 \\ 0.79 \end{pmatrix}$$

It is traditional to normalize this vector by dividing each age-specific reproductive value by that of newborn individuals:

$$V = \frac{V_{raw}}{V_{raw_0}} \qquad V = \begin{pmatrix} 1 \\ 1.54 \\ 2.37 \end{pmatrix}$$

We now have all the data needed to calculate the elasticities of the elements of the cheetah transition matrix:

$$E = \begin{pmatrix} 0 & 0 & 0.13 \\ 0.13 & 0 & 0 \\ 0 & 0.13 & 0.6 \end{pmatrix}$$

If we look carefully through the elasticity matrix $E$ for the Serengeti cheetah population we see that one value (0.6) is clearly larger than the rest. This value corresponds to the adult survival rate in the original transition matrix $A$. It implies that a change in adult survival would have more impact on the rate of population growth by cheetahs than a change of similar proportion of any other demographic parameter. This is a very useful statistic, allowing conservation biologists to identify which demographic parameters have the strongest influence on long-term viability.

## 13.8 Stage-specific models

In many organisms it makes more sense to think about different demographic stages or size classes, rather than specific age classes. This can also be a convenient means of approximating the dynamics of long-lived organisms, by lumping age groups into stages, because often we do not have information on exact ages. Such an approach is known as a Lefkovitch stage-class model (Lefkovitch 1965; Caswell 2001). This involves multiplying stage-specific population densities by a transition matrix ($A$). The top row of $A$ reflects the probability of survival for stage class $i$ multiplied by its fecundity $f_i$. The diagonal reflects the probability of surviving and remaining within stage $i$ $p_i$, while the subdiagonal represents the probability of surviving and growing into the

next stage $g_i$.

$$A = \begin{pmatrix} p_0 & f_1 & f_2 & f_3 & f_4 & f_5 & f_6 \\ g_0 & p_1 & 0 & 0 & 0 & 0 & 0 \\ 0 & g_1 & p_2 & 0 & 0 & 0 & 0 \\ 0 & 0 & g_2 & p_3 & 0 & 0 & 0 \\ 0 & 0 & 0 & g_3 & p_4 & 0 & 0 \\ 0 & 0 & 0 & 0 & g_4 & p_5 & 0 \\ 0 & 0 & 0 & 0 & 0 & g_5 & p_6 \end{pmatrix}$$

When we multiply this Lefkovitch matrix by a vector of stage groups, the use of the two sets of diagonals allows some individuals in each stage to mature into the next while others remain in the same stage as before. Just as we saw for simple age-structured models, the stage-class model predicts geometric increase (or decrease, depending on the magnitude of $\lambda$) after the age structure has equilibrated.

A good example of the application of this kind of model involves the loggerhead sea turtle (*Caretta carreta*), a marine species that lays its eggs in sandy beaches of the southeastern United States. Demographic parameters are difficult to estimate for a long-lived species like the loggerhead, which roams widely across the Atlantic Ocean. Hence, accurate age-specific data are unavailable, as are age-specific estimates of fecundity. Crude data are available, however, on the relative survival rates and fecundities of different stages: eggs, hatchlings, and mature individuals. Additional predictable variation in fecundity stems from body size. Crouse *et al*. (1987) developed a Lefkovitch stage-class model (Box 13.2) to evaluate which of seven life stages would be most responsive to conservation efforts. This is a considerable simplification of the 54 age classes that would be needed for a full Leslie matrix model.

**Box 13.2** The Lefkovitch stage-class model for the loggerhead sea turtle (Crouse *et al*. 1987).

There are seven stages in the model. The youngest (0) represents eggs and hatchlings. The next two (1 and 2) represent small and large juveniles. Sub-adults are represented by stage 3. All individuals beyond stage 3 are capable of breeding. Stage 4 represents novice breeders. The last two stages correspond to young (5) and older (6) adults. Crouse *et al*. (1987) estimated the proportion of individuals growing into the next class by assuming a stable age distribution – perhaps a risky assumption. On this basis, they derived the following Lefkovitch matrix model:

$$p = \begin{pmatrix} 0.0 \\ 0.737 \\ 0.661 \\ 0.691 \\ 0.0 \\ 0.0 \\ 0.809 \end{pmatrix} \qquad g = \begin{pmatrix} 0.675 \\ 0.049 \\ 0.015 \\ 0.052 \\ 0.809 \\ 0.809 \\ 0 \end{pmatrix} \qquad f = \begin{pmatrix} 0 \\ 0 \\ 0 \\ 0 \\ 127 \\ 4 \\ 80 \end{pmatrix}$$

$$A = \begin{pmatrix} p_0 & f_1 & f_2 & f_3 & f_4 & f_5 & f_6 \\ g_0 & p_1 & 0 & 0 & 0 & 0 & 0 \\ 0 & g_1 & p_2 & 0 & 0 & 0 & 0 \\ 0 & 0 & g_2 & p_3 & 0 & 0 & 0 \\ 0 & 0 & 0 & g_3 & p_4 & 0 & 0 \\ 0 & 0 & 0 & 0 & g_4 & p_5 & 0 \\ 0 & 0 & 0 & 0 & 0 & g_5 & p_6 \end{pmatrix} \qquad n^{\langle 0 \rangle} = \begin{pmatrix} 10 \\ 5 \\ 3 \\ 2 \\ 1 \\ 1 \\ 0 \end{pmatrix}$$

## 13.9 Elasticity of the loggerhead turtle model

The largest eigenvalue of the loggerhead sea turtle transition matrix equals 0.95, implying that the population cannot sustain itself (a value of 1.0 is required for sustainability, i.e. a stationary population). Age- or stage-specific models also offer useful insights into possible remedies to counteract such population declines. By modifying vital rates, one can interpret the effectiveness of possible conservation actions that might be taken. In the case of loggerheads, for example, one could protect nesting sites on beaches or alternatively devote larger effort to improving survival while the animals are out at sea. One way to evaluate these options is by calculating elasticities of the transition matrix. The elasticity calculations for the loggerhead sea turtle are shown in Box 13.3.

Changing some demographic parameters obviously has a stronger impact on turtle growth rates than does changing others. The largest elasticities correspond to the probabilities of survival and remaining within the adult and juvenile stage classes. If one had a finite amount of money, energy, and time to devote to conserving this species, it

**Box 13.3** Calculation of elasticities of the Lefkovitch matrix for the loggerhead sea turtle. (Based on data from Crouse *et al*. 1987.)

The stable age distribution for the loggerhead turtle is calculated from the right eigenvector of transition matrix $A$ in Box **13.2**, for which 0.947 is the dominant eigenvalue.

$$W = \begin{pmatrix} 0.21 \\ 0.67 \\ 0.11 \\ 0.01 \\ 3.69 \times 10^{-4} \\ 3.16 \times 10^{-4} \\ 0 \end{pmatrix}$$

In other words, after the loggerhead turtle model has proceeded for a number of years, we will expect to see 21% of the population being composed of eggs or hatchlings, 67% juveniles, and the rest (12%) sub-adults and adults.

For the loggerhead sea turtle, the vector $V$ depicting stage-specific reproductive value is as follows:

$$V = \begin{pmatrix} 1 \\ 1.4 \\ 6 \\ 114.31 \\ 562.07 \\ 500.74 \\ 581.02 \end{pmatrix}$$

With these values we can estimate elasticities for every parameter in the transition matrix:

$$E_{i,j} = \frac{A_{i,j}}{\lambda} \cdot \left( \frac{V_i \cdot W_j}{V \cdot W} \right)$$

$$E = \begin{pmatrix} 0 & 0 & 0 & 0 & 0.01 & 3.3 \times 10^{-4} & 0.04 \\ 0.05 & 0.18 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0.05 & 0.12 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0.05 & 0.14 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0.05 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0.04 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0.04 & 0.23 \end{pmatrix}$$

would be most effectively spent on improving adult or juvenile survival. Interestingly, most conservation effort prior to the paper of Crouse *et al*. (1987) had been devoted to enhancing breeding success on the beaches. Although this was no doubt useful, the elasticity calculations suggest that efforts would have been better spent on improving survival at sea.

Turtle excluder devices (TEDs) can greatly reduce mortality of turtles that get caught accidentally in fish and shrimp trawls. The elasticity calculations suggest that application of TEDs should be the most efficient means of improving the long-term viability of the population. Let us assume that such devices improve survival of old adults from 81% to 95%. Would this be sufficient to ensure long-term viability?

The demographic modified matrix obtained by changing adult survival to 95% leads to a finite rate of increase $\lambda = 1.01$, which is indeed just sufficient to allow sustainability. Hence, strenuous enforcement of TEDs would be sufficient to allow population recovery. Given the slender margin, however, other conservation practices are also called for, such as improved breeding success and enhanced hatchling survival to the juvenile stage. In practice, enhanced usage of TEDs has led to dramatic improvement in loggerhead turtle survival, a genuine conservation success story!

## 13.10 Short-term changes in structured populations

Although the Leslie matrix, Lefkovitch matrix, and geometric models make similar predictions in the long term, they definitely make different ones in the short term, before the age distribution has had a chance to stabilize. This may be particularly important in conservation and management of many wildlife species that tend to be long-lived. Many wildlife populations accordingly have age distributions that are far from stable (Owen-Smith 1990; Coulson *et al*. 2001a, 2003; Lande *et al*. 2002). Under these circumstances, it would be useful to have a reliable means of quantifying which demographic parameters have the greatest short-term impact on population growth. A promising approach has recently been outlined by Fox and Gurevitch (2000), based on use of the full set of eigenvalues and eigenvectors, rather than just the dominant set. Application of this new approach with an endangered cactus species (*Coryphanta robbinsorum*) demonstrated that the key demographic parameters for population growth in the short term differed considerably from those identified by standard elasticity assessment (Fox and Gurevitch 2000).

## 13.11 Environmental stochasticity and age-structured populations

When we link age structure with density dependence and environmental stochasticity, we begin to understand the multiple factors that can influence population dynamics. A well-known example comes from the feral Soay sheep on the St. Kilda archipelago off the coast of Scotland. These sheep, similar in many ways to the ancestral sheep first domesticated by humans, were initially introduced during the second millennium BC. They have roamed wild for decades on several of the St. Kilda islands, the best known of which is the small island of Hirta. A fraction of the Hirta population uses an open, grassy area once occupied by people. Here the pregnant females use abandoned stone huts for shelter during birth. As a consequence, sheep numbers can be counted accurately and a large fraction of the newly born lambs can be caught and marked. Tracking these known individuals over the subsequent years has allowed unusually detailed calculations of age-specific reproduction and survival (Clutton-Brock *et al*. 1997).

The demographic pattern that has emerged from these field studies shows pronounced threshold effects of population density on sheep survival (Fig. 13.4). When

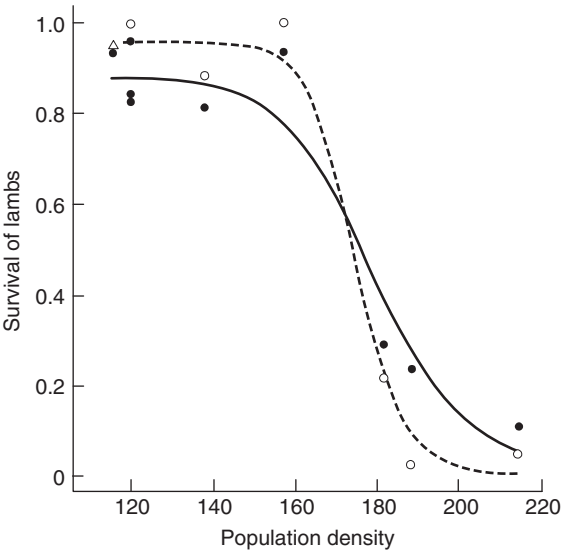


**Fig. 13.4** Survival of Soay sheep lambs on the island of Hirta in relation to adult population density: females (solid line), males (broken line). (After Clutton-Brock *et al.* 1997.)

the population is less than 200 adult sheep, survival of lambs, yearlings, and adults tends to be high: typically > 90% in adults and yearlings and > 80% in lambs. Increase in sheep abundance beyond the threshold tends to be accompanied by a precipitous decline in survival to low levels, sometimes as low as 10%. In order to fully understand the impact of these threshold effects, we need to construct a model that combines density-dependent and age-dependent features (see Box 13.4).

**Box 13.4** Model of the Soay sheep population on St. Kilda.

Threshold effects on mortality can be well described by a sigmoid function:

$$\Psi(i, N) = \frac{p_{\max_i}}{1 + (\alpha_i \cdot N)^{\beta_i}}$$

where $i$ refers to the age group (from 0 for newborns up to 2 for adults), $N$ is the population density of yearlings and adults, $p_{\max}$ is the maximum survival rate, and $\alpha$ and $\beta$ are parameters determining the shape of the sigmoid survival function ($\Psi$). Clutton-Brock *et al.* (1997) estimated the parameters of the $\Psi$ function from several years of data as follows:

$$p_{\max} = \begin{pmatrix} 0.88 \\ 0.94 \\ 0.96 \end{pmatrix} \alpha = \begin{pmatrix} 0.00562 \\ 0.00484 \\ 0.00467 \end{pmatrix} \beta = \begin{pmatrix} 15.3 \\ 9.46 \\ 8.93 \end{pmatrix}$$

Similar sigmoid functions ($\Omega$) can be fitted to age-specific fecundity rates of females:

$$m_{\max} = \begin{pmatrix} 0.335 \\ 0.643 \\ 0.643 \end{pmatrix} \gamma = \begin{pmatrix} 0.00629 \\ 0.00589 \\ 0.00589 \end{pmatrix} \varphi = \begin{pmatrix} 24.1 \\ 14.1 \\ 14.1 \end{pmatrix}$$

$$\Omega(i, N) = \frac{m_{\max_i}}{1 + (\gamma_i \cdot N)^{\varphi_i}}$$

By applying these density-dependent survival and fecundity rates to specific age-classes, we can estimate changes in abundance over time:

$$\begin{pmatrix} n_{0,t+1} \\ n_{1,t+1} \\ n_{2,t+1} \end{pmatrix} = \begin{bmatrix} \sum_i \left( n_{1,t} \cdot \Omega\left( i, \sum_j n_{j,t} \right) \cdot \Psi\left( i, \sum_j n_{j,t} \right) \right) \\ n_{0,t} \cdot \Psi\left( 0, \sum_j n_{j,t} \right) \\ n_{1,t} \cdot \Psi\left( 1, \sum_j n_{j,t} \right) + n_{2,t} \cdot \Psi\left( 2, \sum_j n_{j,t} \right) \end{bmatrix}$$

Simulation models constructed with threshold survival and fecundity effects (Fig. 13.5) generate regular fluctuations of Soay sheep at 6-year intervals (Fig. 13.6), qualitatively similar to the patterns seen by the real population (Fig 13.7) (Grenfell *et al*. 1992). The model does not capture all of the variability in sheep abundance observed on St. Kilda. Like all models, it leaves out many important features. It has

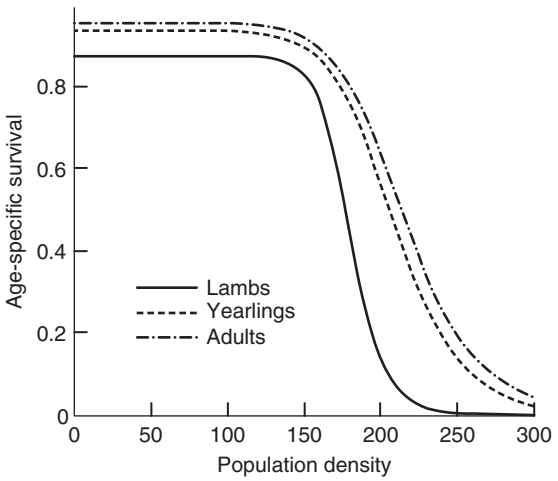


**Fig. 13.5** Sigmoid survival functions in relation to the population density of adult + yearling Soay sheep, for adults (dashed-dotted line), yearlings (dotted line), and lambs (solid line), estimated by Clutton-Brock *et al*. (1997).

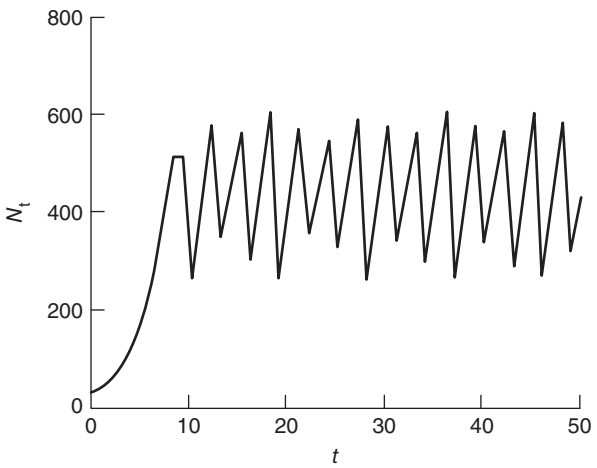


**Fig. 13.6** Simulated dynamics of an age-structured population with sigmoid survival and fecundity functions with the same parameters as those of the Soay sheep population on the island of Hirta. (After Clutton-Brock *et al*. 1997.)

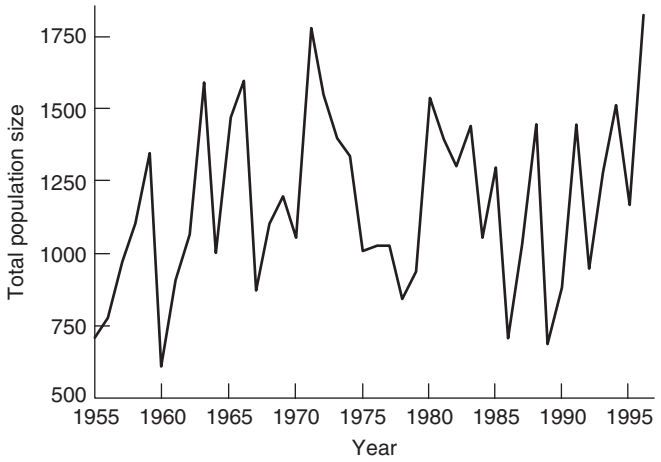


**Fig. 13.7** Observed variation in the population of Soay sheep over the entire St. Kilda archipelago. (After Clutton-Brock *et al.* 1997.)

no direct link with food supply or disease, both of which are important in shaping dynamics. Catastrophic mortality is largely caused by starvation, and vulnerability to starvation is exacerbated by high nematode infestation in the intestinal tract of individual sheep (Gulland 1992; Clutton-Brock *et al.* 1997). Nonetheless, the model clearly demonstrates that the combination of age structure and threshold effects predispose the Soay sheep population to recurrent cycles in abundance.

Strong effects of weather variation can influence the population dynamics of Soay sheep (Grenfell *et al.* 1998; Coulson *et al.* 2001a). Populations of sheep on adjacent, isolated islands tend to be loosely synchronized, because they share a common climate (Grenfell *et al.* 1998). Although density-dependent processes regulate Soay sheep, the precise pattern of regulation is strongly affected by age structure. Different age groups vary in their degree of density dependence and sensitivity to weather conditions (Catchpole *et al.* 2000; Coulson *et al.* 2001a). As a result, a population dominated by young animals would have quite different population dynamics in the short term from one with a more equitable distribution of age groups. The mix of age groups on any of the islands is highly changeable and slight modifications in age structure alter the dynamic consequences of density-dependent processes (Coulson *et al.* 2001a). The Soay sheep example illustrates how populations can fluctuate through a combination of (i) stochastic environmental effects, (ii) nonlinear demographic responses, and (iii) delays that arise through a complex age structure.

## 13.12 Summary

The dynamic behavior of a population – whether it increases, decreases, or remains constant – is determined by its age- or stage-specific mortality and fecundity rates interacting with the underlying distribution of ages or stages in the population. A wide variety of techniques are available for estimating age-specific parameters, summarized in the life table. When age-specific rates of fecundity and survivorship remain constant, the population's age distribution assumes a stable form, even though its size may be changing. These demographic parameters determine the rate of population change over time, forming the logical basis for many conservation and management decisions.

The long-term rate of population change can be calculated through use of a transition matrix composed of these vital rates. Determination of the elasticity of the rate of population change due to slight modifications of the vital rates can be a useful means of

evaluating alternate conservation and management options, as illustrated by the case studies with cheetahs and loggerhead turtles.

In most wildlife species, population dynamics over the long term will be strongly influenced by age structure, density dependence, and how each of these parameters is affected by environmental stochasticity. These synergistic effects are well demonstrated by the Soay sheep population off the coast of Scotland.