

terminology has been developed to explain this phenomenon. For example, a **genet** is an individual that has arisen from a seed. A **ramet** is a new plant that is a clone but which has arisen through vegetative propagation and is now a completely independent plant with its own roots and shoots. Thus a population of grasses may consist of several genets, each of which has several ramets. Clonal populations may proliferate indefinitely without flowering. This has led to some fascinating life cycles such as that of the giant bamboo (*Phyllostachys bambusoides*), in which clones of perennial ramets proliferate, forming large populations that flower only once every 120 years (Janzen 1976). All of the clonal ramets flower simultaneously and then the entire population dies, leaving behind only seeds with which to found the next population. Studies conducted since the great 1988 fire in Yellowstone National Park have forced biologists to revise the conventional wisdom that aspen (*Populus tremuloides*) does not reproduce by seed, but spreads by cloning. Instead Turner *et al.* (2003) suggest that new genets of aspen as well as some of the perennial herbs of the forest floor are produced after fires, but recruitment of new individuals (ramets) during fire-free intervals is primarily through asexual reproduction.

In the sections below, as we refer to age-specific traits of survivorship or fertility, keep in mind that many plant and animal populations would often require a rather different approach in which we examine survivorship and fertility by size class or by stage in the life cycle.

4.2 Survivorship

The construction of a life table begins by gathering information on survivorship by age class. This sounds simple, but is easier described than actually done. For example, one method is to study a **cohort** of individuals all born at the same time, and follow the survivorship of these individuals until the last member of the cohort dies. At the beginning of such a study, it would be necessary to locate and mark all newborn individuals. Subsequently, one would need to verify when each individual died. Individuals that simply disappeared could not be assumed to have died; they might have emigrated. Studies of cohorts are obviously best done on small populations and on populations that move about in a predictable way. The advantage of studying a cohort is that one knows the exact age of each individual. The disadvantage is that such a study lacks generality, in that cohorts born in different years may have different survivorship schedules. In addition to the difficulties one might encounter in actually marking and gathering information on all members of a cohort, there are also practical problems. A cohort study on most species of turtles, for example, would require the entire professional life span of the investigator (picture a student waiting 50 years to finish her PhD dissertation). A life table developed in this manner is known as a **fixed-cohort, dynamic, or horizontal life table**.

A second approach is to locate and examine all of the dead individuals in a population during some defined period of time. We would need a method for estimating the age of the animals or plants at death. This approach to the construction of a life table assumes that the rates of survival in the population are fairly constant. If this is not the case, age-specific mortality rates will be confused with year-to-year variation in mortality of the overall population. Data gathered in this manner produce a **static, vertical, or time-specific life table**.

A third approach is to collect life-history data for several cohorts over as long a period as possible. In most populations there is a large difference between juvenile and adult

Table 4.1 Survivorship data for males born between 1800 and 1890, taken from the Fairfax City Cemetery, Fairfax, Virginia.

Age category	Number who died in the age category	Number alive at the beginning of the age class	S_x based on a cohort of 1000	Survivorship, l_x (Proportion of original cohort alive at the beginning of the age category)
0-1	0	207	1000	1.000
1-4	1	207	1000	1.000
5-9	0	206	995	0.995
10-14	2	206	995	0.995
15-19	2	204	986	0.986
20-24	4	202	976	0.976
25-29	0	198	957	0.957
30-34	1	198	957	0.957
35-39	0	197	952	0.952
40-44	5	197	952	0.952
45-49	2	192	928	0.928
50-54	12	190	918	0.918
55-59	9	178	860	0.860
60-64	18	169	816	0.816
65-69	24	151	729	0.729
70-74	33	127	614	0.614
75-79	33	94	454	0.454
80-84	35	61	295	0.295
85-89	20	26	126	0.126
90-94	3	6	29	0.029
95-99	2	3	14	0.014
100-104	1	1	5	0.005
105-109	0	0	0	0.000
Total population	207			

survivorship. Therefore, even though survivorship data on adults are often relatively easy to gather, such data do not apply to the juvenile age classes. Depending on the age when reproduction begins, it is possible to find the growth rate of the population without specific data on juvenile survivorship, as described later in the chapter.

No matter how the data are gathered, the objective is to produce an estimate of age-specific survivorship and fertility. In human demography, age-specific survivorship is based on a theoretical cohort of 1000 individuals. If we let S_x equal the number of individuals surviving to age x , we set S_0 equal to 1000. Then, S_1 = the number of individual surviving to age 1, S_2 = the number surviving to age 2, etc. Table 4.1 is based on data gathered by an ecology laboratory from the Fairfax City (Virginia) cemetery. In this case 207 male grave-

stones were examined and the ages at death calculated. (Data were gathered only from

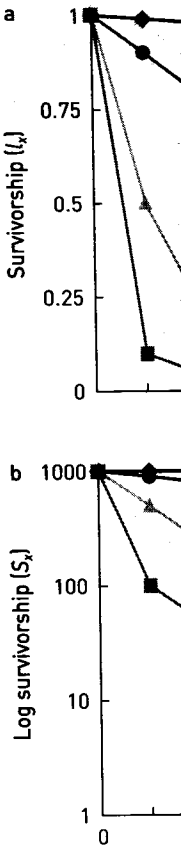


Figure 4.1 Sur

graves in which humans are so is to use the number of survivors of 1000 by dividing each number in l_x . Each value in to a given age population die the probability,

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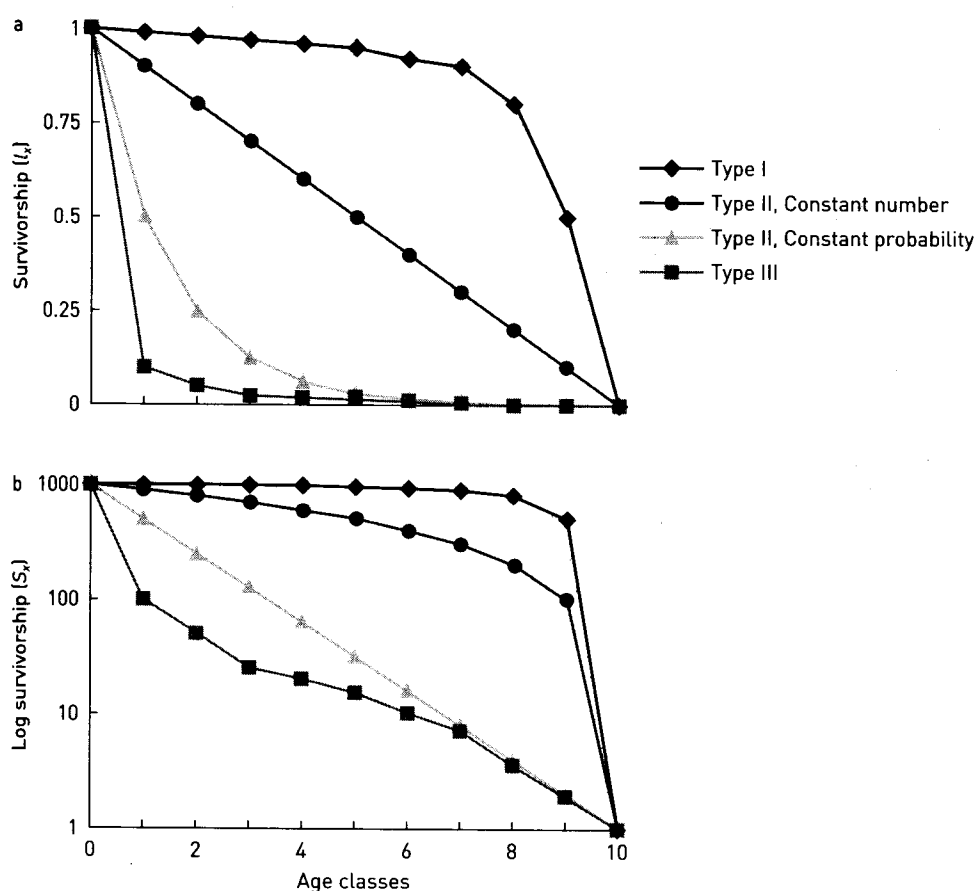


Figure 4.1 Survivorship "type" curves: (a) on an arithmetic scale; (b) on a log scale.

graves in which the birth date was between 1800 and 1890. Why was this done?) Because humans are so long-lived, the data were placed into five-year age intervals. The first step is to use the number who died in each age interval (column 2) to produce column 3, the number of survivors by age class. Next, we normalize the population to a theoretical cohort of 1000 by dividing each number by 207 and multiplying by 1000. This produces the S_x column. However, in most ecological studies we do not, in fact, use the S_x data. Instead, each number in the S_x column is divided by 1000 to produce the survivorship function, l_x . Each value in the l_x column stands for the proportion of the population that survives to a given age, x . It is measured from birth until the last or oldest member of the population dies. l_x is known as **age-specific survivorship** and can be thought of as the probability, at birth, of living to a specific age class. By definition, $l_0 = 1.00$.

The survivorship table is used to construct the survivorship curves found in all ecology textbooks. In a survivorship curve, age (x), the independent variable, is graphed against survivorship. The y -axis may be on a straight arithmetic scale; however, many authors prefer a log (base 10) scale for survivorship. Pearl (1927) introduced the idea that biological populations routinely fit one of three "types" of survivorship curves (Fig. 4.1a). The type I curve, known as the "death at senescence" curve, is characterized by excellent survivorship at all ages from birth until "old age," at which time the death rate rapidly accelerates

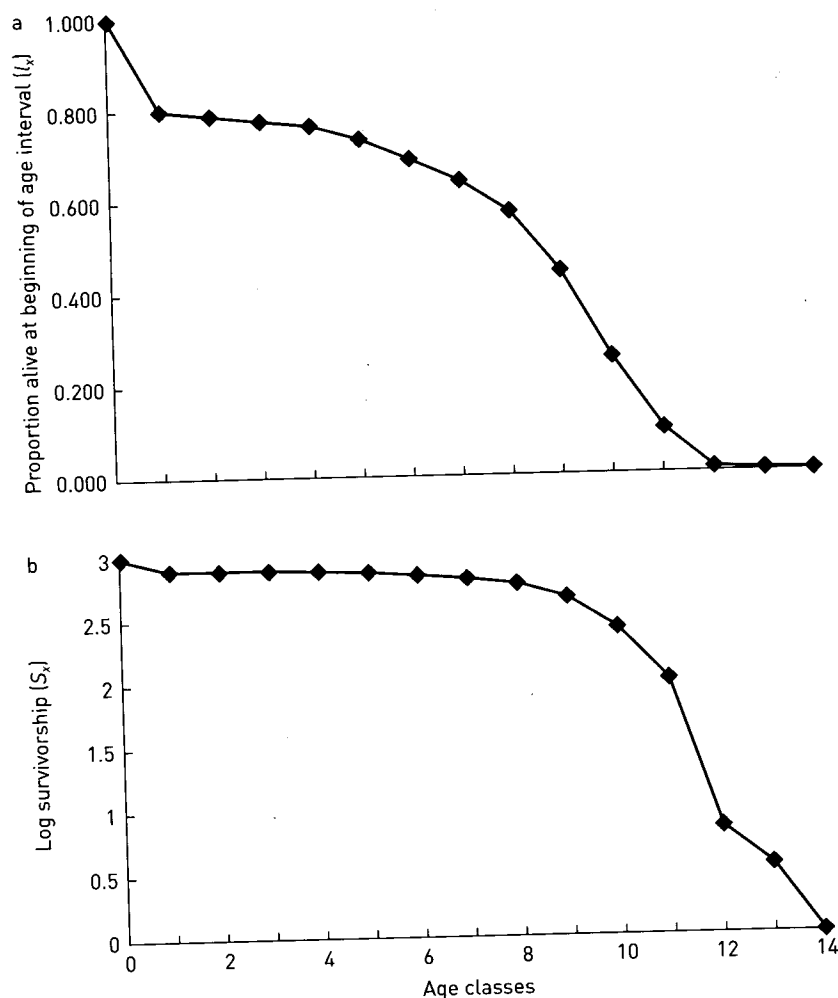


Figure 4.2 Dall sheep (*Ovis dalli*) in Denali National Park, Alaska. (a) Survivorship (l_x); (b) log of survivorship (S_x). After Deevy (1947).

and survivorship plummets. The type II curve is linear and assumes that either a constant number or a constant proportion of the population dies in each age interval. Examine Fig. 4.1. When survivorship is expressed on an arithmetic scale, a constant number of deaths per age interval produces a linear curve. When log to the base ten of survivorship is used (Fig. 4.1b), the constant probability of death per age interval produces a straight line. Finally, the type III curve applies to the vast majority of biological populations. In this curve there is very high mortality among the juvenile age classes while adult survivorship is relatively high. This is illustrated most dramatically in Fig. 4.1a, using the arithmetic scale for survivorship.

How realistic are these three survivorship "types?" Probably few populations exactly match any particular one. Furthermore, as found by Petranksa and Sih (1986) for the salamander species *Ambystoma texanum*, survivorship curves may vary from year to year and place to place for the same species. (Recall our discussion in Chapter 1 of population viability analysis, in which we emphasized that demographic traits are subject to both temporal

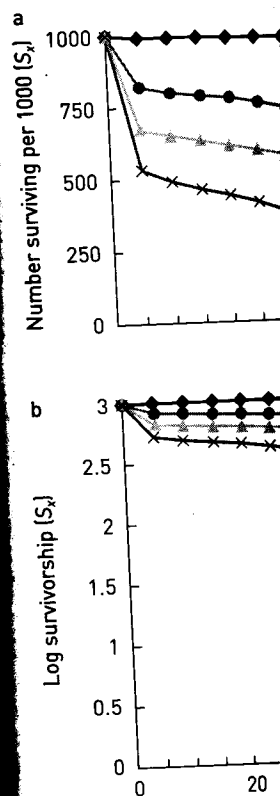


Figure 4.3 Human survivorship curves for two modern United States populations. (a) Number surviving per 1000 (S_x); (b) log survivorship (S_x). After Lotka (1956).

and spatial variability of the three types is such as *Drosophila*. survivorship until the simultaneously (Hut

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While modern h distant past, living to 500 of the original expectancy at birth the age of 80 (Pete twentieth century, t lish populations, a around 40 years in scale, however, the

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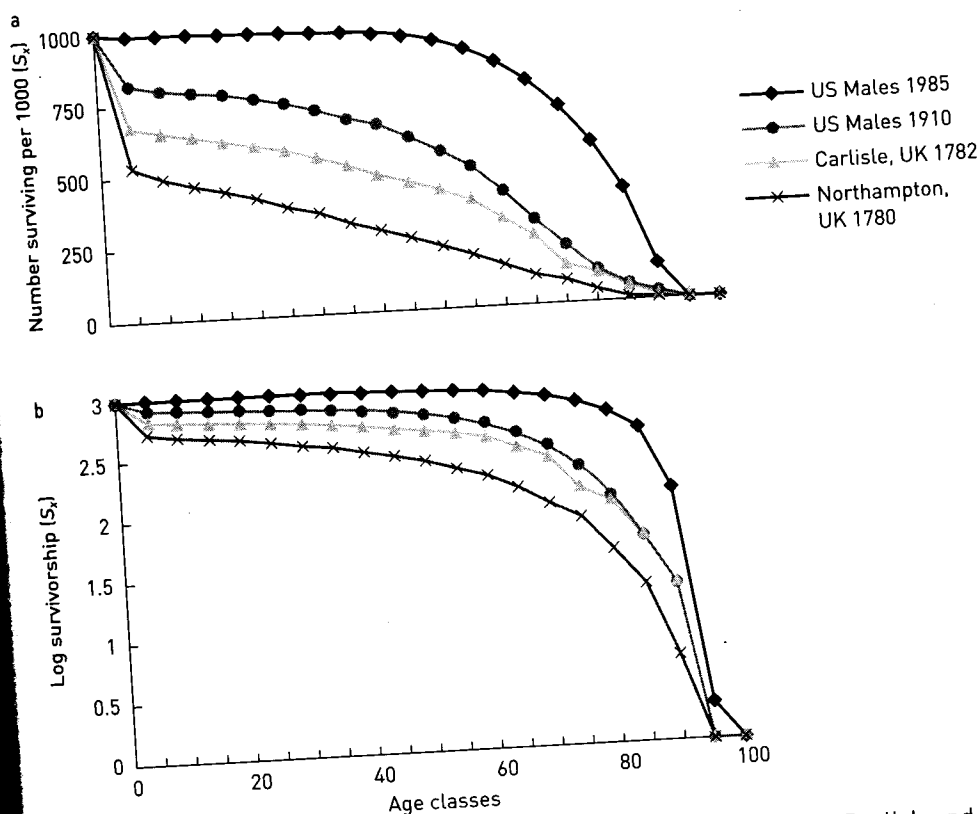


Figure 4.3 Human survivorship curves from two eighteenth-century English and two modern United States populations: (a) on an arithmetic scale; (b) on a log scale. After Lotka (1925) and Peters and Larkin (1989).

and spatial variability.) However, we can make some general comments. The least realistic of the three types is type I. A type I curve applies to laboratory populations of animals such as *Drosophila*. If provided with ample food, the population has a high rate of survivorship until the end of its maximum life span, when individuals die more or less simultaneously (Hutchinson 1978).

Natural populations of mammals such as Dall mountain sheep (*Ovis dalli*) (Deevy 1947), and many African ungulates (Caughley 1966), have a type I survivorship curve, although notice that 20% of the Dall sheep die in the first year of life (Fig. 4.2).

While modern human populations have a type I survivorship curve, in the not-so-distant past, living to a ripe old age was not assured (Fig. 4.3). By looking for the age where 500 of the original 1000 in a population are still alive, we have an idea of the average life expectancy at birth (Fig. 4.3a). For the modern (1985) US population, this figure is after the age of 80 (Peters and Larkin 1989). By contrast, for US males living early in the twentieth century, this figure was less than 60 (Lotka 1925). For eighteenth-century English populations, average life expectancy was less than 10 years in Northampton and around 40 years in Carlisle (Lotka 1925)! When these same values are plotted on a log scale, however, they all approximate a type II survivorship curve (Fig. 4.3b).

In order for an organism to have a type I survivorship curve, all stages of the life history must be more or less equally vulnerable to predation or other causes of death. Birds,

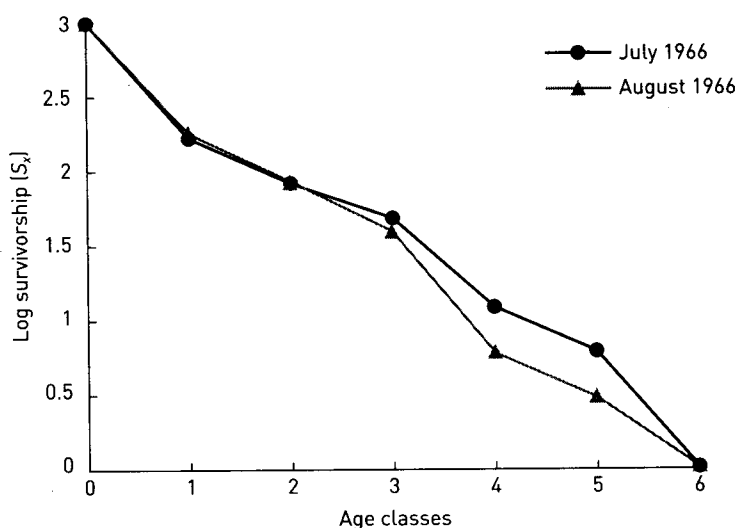


Figure 4.4 Log survivorship for two cohorts of white-crowned sparrows (*Zonotrichia leucophrys*). Based on Baker *et al.* (1981).

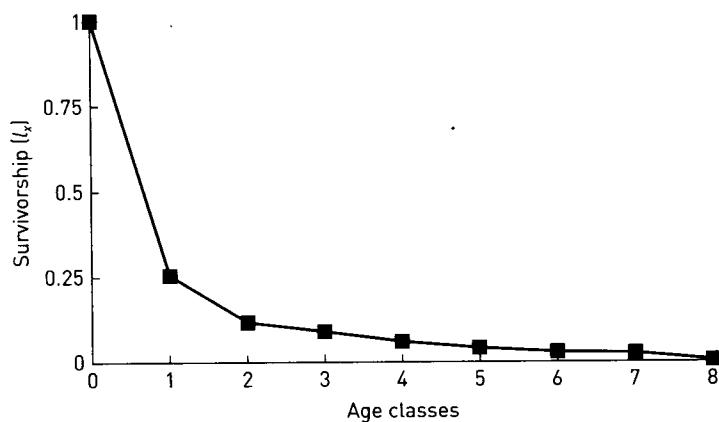


Figure 4.5 Survivorship curve for a gray squirrel (*Sciurus carolinensis*) population in North Carolina. Based on Barkalow *et al.* (1970).

especially the adult stages, are most commonly cited as having a type II survivorship curve. For example, when Gibbons (1987) examined longevity records of vertebrates in captivity, only birds displayed a type II survivorship curve on an arithmetic scale. In a study of white-crowned sparrows (*Zonotrichia leucophrys*) (Fig. 4.4) Baker *et al.* (1981) found a type II survivorship curve on a log scale, which indicates a more or less constant probability of death, irrespective of age. The maximum life span was 49 months in this species. Botkin and Miller (1974), however, argued that birds do not, in fact, have an age-independent mortality rate. The survivorship curve for the sooty shearwater (*Puffinus griseus*), based on an arithmetic scale, appears to be type II. However, Botkin and Miller showed that, on closer examination, while the mortality rate in the early age classes was 0.07 per year, there was an increase in the mortality rate of 0.01 per year. They concluded that mortality was not in fact age-independent in the sooty shearwater, nor indeed in most species of birds.

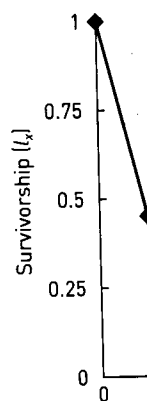


Figure 4.6 Survivorship curve for a population of golden lion tamarins (*Leontideus rosalia*). From J. Ballou.

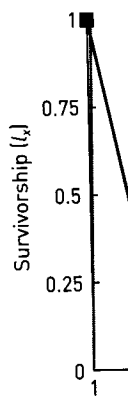


Figure 4.7 Survivorship curve for a population of gray squirrels (*Sciurus carolinensis*). Based on Leverich *et al.*

The type III survivorship curve, characterized by high mortality in the early age classes followed by high survivorship in the adult stages, is found in many populations from barn swallows to elephants. Some populations of mammals, such as gray squirrels and golden lion tamarins (see above), and some fish (e.g., *Salmo trutta*) have type III survivorship curves (e.g., Anderson *et al.* 1987).

Actually, most species have a type II survivorship curve. On an arithmetic scale, survivorship drops from 1.0 at age 0 to 0.5 at age 1, and then continues to decline. On a log scale, survivorship is down to 0.5 at age 1, and then continues to decline. On an arithmetic scale, survivorship has been shown to be almost a year old (e.g., *Salmo trutta*). On a log scale, survivorship has been shown to be almost a year old (e.g., *Salmo trutta*). Although survivorship is almost a year old (e.g., *Salmo trutta*), survivorship is almost a year old (e.g., *Salmo trutta*), and nothing is gained.

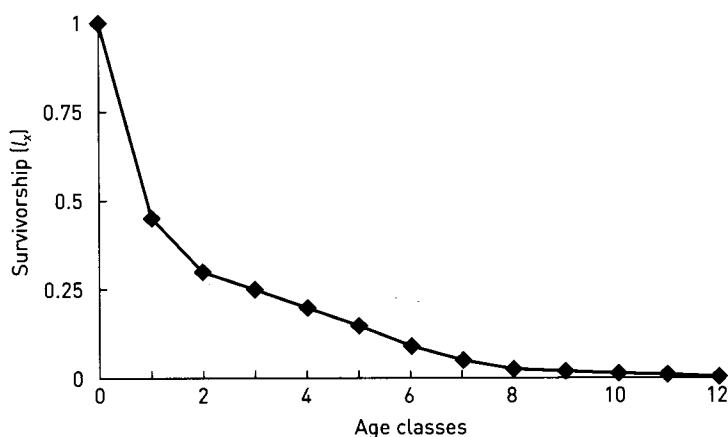


Figure 4.6 Survivorship in captive female golden lion tamarins (*Leontopithecus rosalia*). From J. Ballou (personal communication).

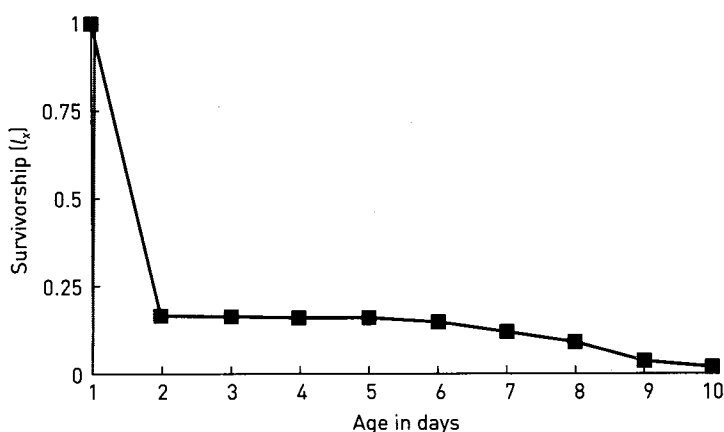


Figure 4.7 Survivorship schedule for *Phlox drummondii* on an arithmetic scale. Based on Leverlich and Levin (1979).

The type III survivorship curve, which features heavy mortality among young age classes followed by good to excellent adult survivorship, applies to most biological populations from barnacles to sea turtles to plants (Hutchinson 1976). Even medium-sized mammals, such as gray squirrels (*Sciurus carolinensis*) (Fig. 4.5; Barkalow *et al.* 1970) and golden lion tamarins (*Leontopithecus rosalia*) (Fig. 4.6; Jonathan Ballou, personal communication) have type III survivorship curves, as do most amphibians such as *Ambystoma tigrinum* (e.g. Anderson *et al.* 1971).

Actually, most species do not follow any one of the type curves precisely, especially when an arithmetic scale is used. For example, in *Phlox drummondii* (Leverlich and Levin 1979) survivorship drops from 1.00 to 0.67 in the first 63 days after germination. After 124 days survivorship is down to less than 0.30. Mortality is minimal thereafter until the plants are almost a year old (Fig. 4.7). Yet this plant, when its survivorship is plotted on a logarithmic scale, has been used as an example of a type I curve (Smith 1996). Therefore, although survivorship curves are extremely useful in order to visualize the large amount of data in a life table, there is little agreement as to what constitutes a survivorship "type," and nothing is gained by attempting to fit a life table to any of the three "type" curves.

Table 4.2 Fertility data from 1985 US Vital Statistics. Fertility is based on the average number of daughters born in five-year age intervals.

Age class	Mean number of female offspring per female, m_x
0-1	0
1-5	0
5-10	0
10-15	0
15-20	0.025
20-25	0.250
25-30	0.500
30-35	0.150
35-40	0.100
40-45	0.010
45-50	0
50-55	0
55-60	0
60-65	0
65-70	0
70-75	0
75-80	0
80-85	0
85-90	0

4.3 Fertility

The other half of the life table is the fertility column, m_x . Here each value represents the average number of female offspring produced per female of a given age. Again, gathering accurate data on fertility in the field is problematic for many populations. In order to simplify calculations, we count only the number of females. That is, the values are mean numbers of females by age class. Fertility, like survivorship, can be graphed as a function of age, and the resultant fertility curve is usually triangular or rectangular in shape. For example, Table 4.2 illustrates human fertility based on 1985 United States Vital Statistics (Peters and Larkin 1989). Age classes until age 15 are usually termed, "pre-reproductive." Ages 15 to 45 are considered the reproductive age classes. Figure 4.8 illustrates the usual triangular shape, with maximum reproduction occurring in the 25- to 30-year age classes. After age 45, fertility falls back to zero. These are the post-reproductive age classes (modern medical science, however, is pushing the normal boundary of reproduction past 45 years). On the other hand, the North Carolina gray squirrel population (Table 4.3) would have a rectangular shape if fertility were graphed against age.

As usual, when populations are sampled, data do not necessarily follow generalized trends. For example, in a study by Grant and Grant (1992) on the cactus ground finch (*Geospiza scandens*), the fertility schedule had a very irregular shape, dropping radically in the seventh year and showing an unexpected spike in the twelfth year (Fig. 4.9). In this

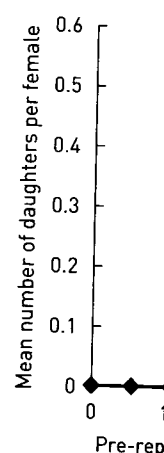


Figure 4.8 Human fertility data from Peters and Larkin (1989).

Table 4.3 Life table for the North Carolina gray squirrel (Barkalow et al. 1970).

Age	l_x
0	1.000
1	0.253
2	0.116
3	0.089
4	0.058
5	0.039
6	0.025
7	0.022
8	0

case, environmental variation (e.g., in *cynocephalus*) also have

The sum of the m_x coefficients represents the average number of offspring produced through the last reproductive age class.

The two pillars of a life table are survivorship and fertility. The hours of fieldwork are not always equal. Once the table is produced, the analysis is straightforward, although all of them assume

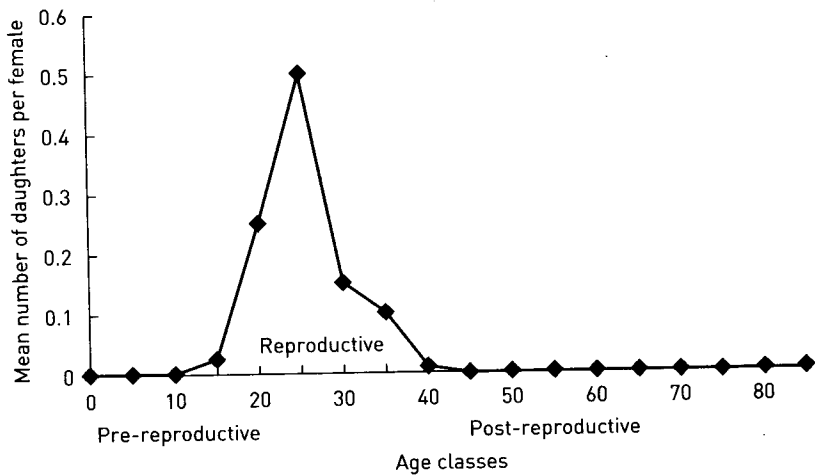


Figure 4.8 Human fertility for the population of the United States, 1985. From Peters and Larkin (1989).

Table 4.3 Life table for a gray squirrel population from North Carolina [Barkalow *et al.* 1970]. (For explanation of symbols see text.)

Age	l_x	m_x	p_x	q_x	$l_x m_x$
0	1.000	0	0.253	0.747	0
1	0.253	1.28	0.458	0.542	0.324
2	0.116	2.28	0.767	0.233	0.264
3	0.089	2.28	0.652	0.348	0.203
4	0.058	2.28	0.672	0.328	0.132
5	0.039	2.28	0.641	0.359	0.089
6	0.025	2.28	0.880	0.120	0.057
7	0.022	2.28	0	1.00	0.050
8	0	0	-	-	0
					$R_0 = 1.119$

case, environmental variation dominated the fertility schedule. Amboseli baboons (*Papio cynocephalus*) also have an irregular fertility schedule (Alberts and Altmann 2003).

The sum of the m_x column defines the **gross reproductive rate** (GRR). This number is the average number of female offspring produced by a female that survives at least through the last reproductive age class:

$$GRR = \sum m_x \tag{4.1}$$

The two pillars of a life table are the survivorship (l_x) and fertility (m_x) columns. Long hours of fieldwork are necessary to gather the data in order to produce such a life table. Once the table is produced, many other calculations and projections are possible, although all of them assume that the survivorship and fertility columns remain constant.

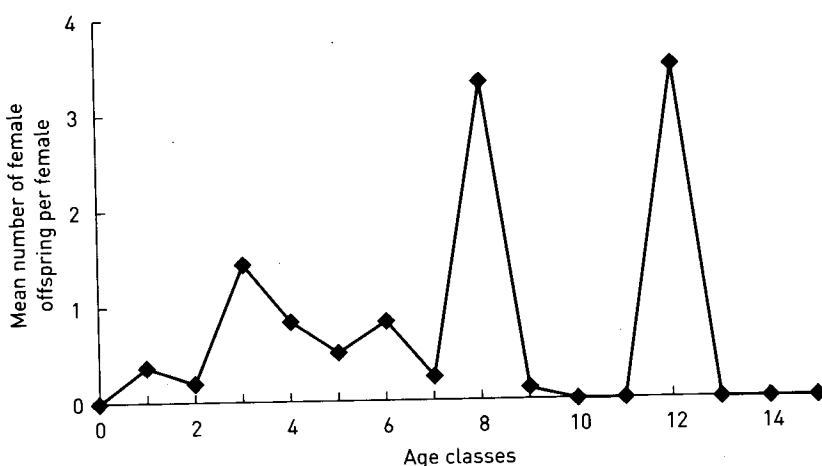


Figure 4.9 Fertility schedule of the cactus ground finch (*Geospiza scandens*). From Grant and Grant (1992).

From the l_x column we can develop two parallel columns, which provide information on how survivorship and mortality rates change with age. Consider Table 4.3. The l_x column is based on the probability, at birth, of surviving to a given age class. The p_x column, by contrast, is the **age-specific probability of surviving to the next age class**. That is, p_2 tells us the probability that an individual who has survived to the age of two will survive to be three years old. Similarly, p_4 would tell us the probability that a four-year-old lives to age five. These p_x values are critically important when we want to project future population growth, as will become clear later in this chapter. p_x is calculated according to the formula:

$$p_x = \frac{l_{x+1}}{l_x} \quad (4.2)$$

For example, in Table 4.3, we see that $p_0 = l_1$, since $p_0 = 0.253/1.000$ (l_0) = 0.253. $p_1 = 0.116/0.253 = 0.458$, and so on. Notice that $p_7 = 0$, since no seven-year-old squirrel lives to be eight years old. p_8 is undefined and is the equivalent of dividing zero by zero.

The companion value to p_x is q_x , which is the proportion of the population that has survived to a given age, x , but which will die in the next time or age interval. q_x is simple to calculate since it is equal to $1 - p_x$ (Eqn. 4.3). This is based on the idea that $p_x + q_x = 1.0$. We recognize only two states of being, alive or dead.

$$q_x = 1 - p_x \quad (4.3)$$

4.4 Mortality curves

Caughley (1966, 1977) and others found that mortality curves (q_x) for female mammals, such as Orkney voles (*Microtus arvalis*) (Leslie *et al.* 1955), toque monkeys (*Macaca sinica*) (Dittus 1977), buffalo (*Syncerus caffer*) (Sinclair 1977), Himalayan thar (*Hemitragus*

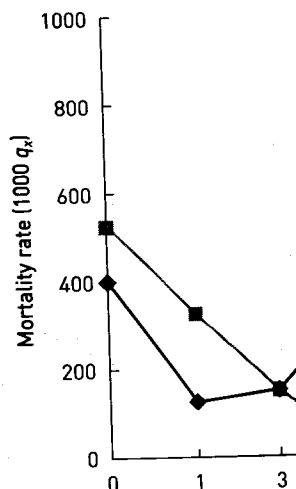


Figure 4.10 Mortality curve. Data from Jarman and

jemlahicus), domestic sheep, and many other mammals follow a U-shaped pattern. Early in life, young animals usually have high mortality rates. In the final phase of life, old animals usually have high mortality rates. (1980) suggested that in many mammals, males have a spike of mortality at old age (e.g., *melampus*) and toque monkeys. These high mortality rates are due to senescence, or the process of aging, and to leave the natal group.

Interestingly, a similar pattern is seen in United States females, with high mortality rates until age 15. Thereafter, mortality rates from the age of 15 to age 65 are exactly those of the young. The greater mortality in the young is due to senescence and/or due to dispersal. Or are there other reasons for a slower rate than those of the young?

4.5 Expectation of life

Another statistic of interest is the age-specific expectation of life.

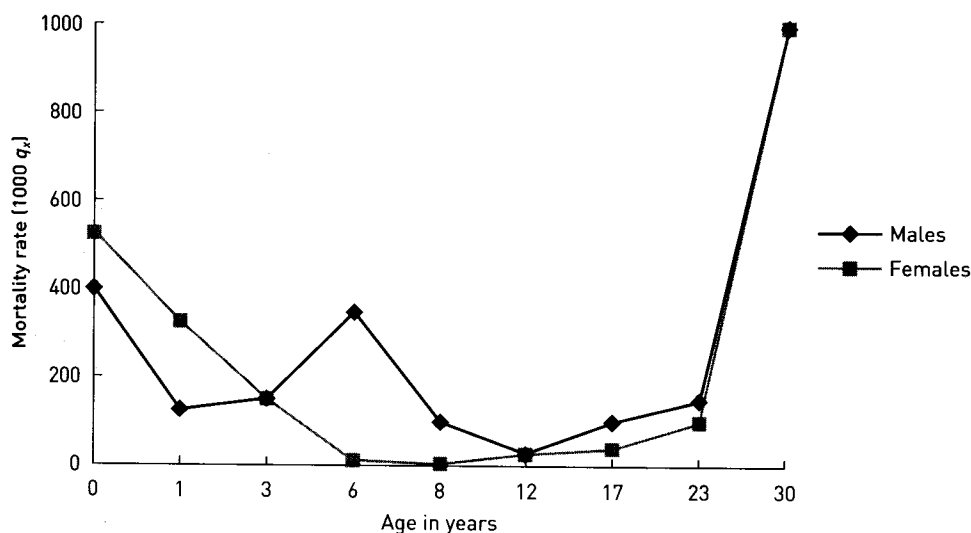


Figure 4.10 Mortality curves for male and female impala (*Aepyceros melampus*). Data from Jarman and Jarman (1973); analysis from Ralls *et al.* (1980).

jemlahicus), domestic sheep (*Ovis aries*), Dall mountain sheep, and elk (*Cervus elaphus*) all follow a U-shaped pattern (Fig. 4.10). The U-shape is the result of the fact that juvenile phases usually have high mortality, but they are coupled with adult phases that have low mortality. In the final phases of life mortality increases (the senescent phase). Ralls *et al.* (1980) suggested that in polygynous species, although females show the U-shaped pattern, males have a spike of mortality in sub-adult to young adult age classes. Impala (*Aepyceros melampus*) and toque monkeys, for example, illustrate this pattern. These higher male mortality rates are due to male–male competition for mates, and the tendency for males to leave the natal group in many species (Ralls *et al.* 1980).

Interestingly, a similar pattern can be found for the United States human population (Fig. 4.11). United States Vital Statistics for 1986 (Anonymous 1988) have a U shape for females, with high mortality in the first year of life, followed by a low rate of mortality until age 15. Thereafter the mortality increases throughout life. Males show higher mortality rates from the age of one onwards. More striking, however, is that the largest separation in mortality rates between the sexes occurs from the ages of 15 to 30. These age classes are exactly those discussed by Ralls *et al.* (1980), in which male mammals suffer greater mortality in the sub-adult to early-adult age classes. Do human males, like other mammals, suffer these higher mortality rates due to male–male competition for females and/or due to dispersal away from the parental home, as Ralls *et al.* (1980) have suggested? Or are there other reasons, such as the suggestion that human male brains mature at a slower rate than those of females (Thompson *et al.* 2000)?

4.5 Expectation of life

Another statistic of interest to demographers, ecologists, and even to non-scientists is the age-specific expectation of life. The question to be addressed is, what is the average life

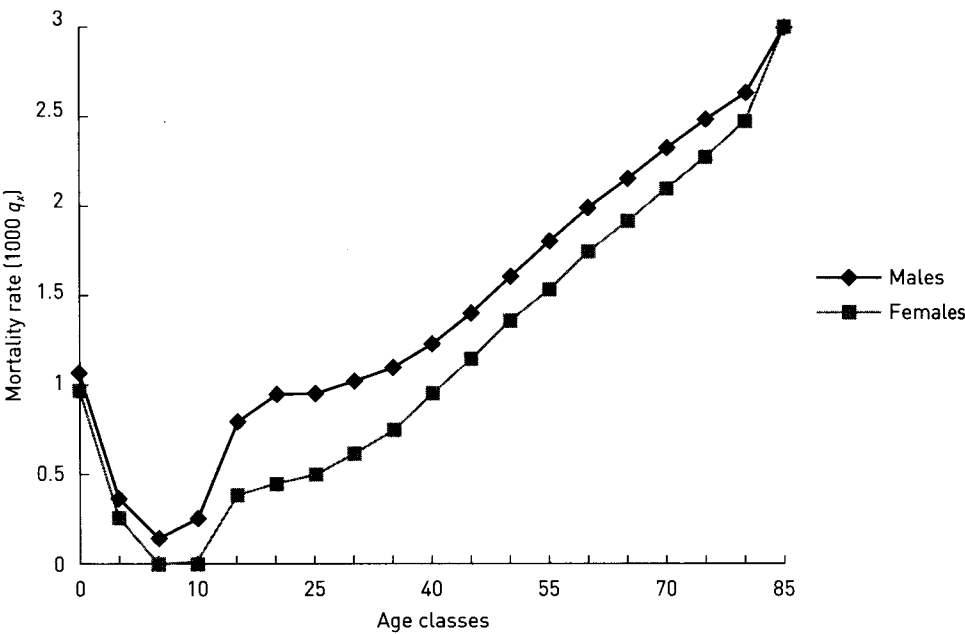


Figure 4.11 Mortality curves for United States human population, based on 1986 vital statistics (Anonymous 1988).

expectancy of an individual of a given age, x ? The survivorship table allows us to directly read the average life span at birth. We simply look for the age at which l_x equals 0.50. However, average expectation of life is age-specific. Obviously, if life expectancy at birth for a human male is 75 years, a male who has survived to be 65 years old should, on average, live well beyond 75. In fact recent data suggest that a 65-year-old human male can look forward to an average of at least 15 more years of life.

Age-specific life expectancy is measured by taking the area under the survivorship curve beyond an age x , and dividing by the number or proportion of survivors of that age, x . In theory, using integral calculus, expectation of life, e_x to the last age class (w) is found using the formula:

$$e_x = \frac{\int_x^w l_x dx}{l_x} \tag{4.4}$$

In practice we use discrete age classes. The survivorship between ages x and $x + 1$, if the age interval is reasonably small, is estimated as follows:

$$L_x = \frac{l_x + l_{x+1}}{2} \tag{4.5}$$

Table 4.4 Calculations

Age, x	
0	
1	
2	
3	
4	
5	
6	
7	
8	

L_x is the mean age, an organism curve for an individual is estimated as:

Therefore exp

In the hypoth two years ($l_x = 0$ 1.46 years.

4.6 Net repro of increase

Once we have th rate statistics w ductive rate, R_0 with discrete ge lation per gener per female in th the fertility and $l_x \times m_x$ is found population gro is the sum of th

Table 4.4 Calculation of average age-specific life expectancy.

Age, x	l_x	L_x	T_x	Expectation of life, e_x
0	1.000	0.850	2.180	2.18
1	0.700	0.600	1.330	1.90
2	0.500	0.400	0.730	1.46
3	0.300	0.200	0.330	1.10
4	0.100	0.075	0.130	1.30
5	0.050	0.035	0.055	1.10
6	0.020	0.015	0.020	1.00
7	0.010	0.005	0.005	0.50
8	0	0	0	0
$\Sigma = 2.18$				

L_x is the mean survivorship for any particular age interval, and assumes that, on average, an organism dies halfway between two age classes. The area under the survivorship curve for an individual of a given age, x , to the age, w , at which the oldest individual dies, is estimated as:

$$T_x = \sum_x^w L_x = \sum_x^w \frac{l_x + l_{x+1}}{2} \quad (4.6)$$

Therefore expectation of life is estimated by Equation 4.7:

$$e_x = \frac{T_x}{l_x} \quad (4.7)$$

In the hypothetical example in Table 4.4 we see that at birth the expectation of life is two years ($l_x = 0.50$). But the average two-year-old individual can expect to live another 1.46 years.

4.6 Net reproductive rate, generation time, and the intrinsic rate of increase

Once we have the basic life table, we are in a position to calculate the same types of growth-rate statistics we discussed in the first two chapters. The first of these is the net reproductive rate, R_0 . This is an equivalent to the R (Eqn. 1.4) we developed for populations with discrete generations. The net reproductive rate represents the increase in the population per generation, and is defined as the mean number of female offspring produced per female in the population per generation. This value is found by incorporating both the fertility and survivorship functions of the life table. For each age class the product of $l_x \times m_x$ is found. This product is the contribution a particular age class is making toward population growth per generation. The net reproductive rate for the population as a whole is the sum of these products for all age classes:

$$R_0 = \sum l_x m_x \quad (4.8)$$

In Table 4.3 the calculated net reproductive rate for the gray squirrel population is 1.119. This means that the average female squirrel replaces herself with 1.119 female squirrels per generation. As in the case of the net reproductive rate for non-overlapping populations, an $R_0 > 1$ means that the population, according to the life table, has the potential to increase every generation. The opposite is also true: an $R_0 < 1$ means that the population is decreasing every generation.

Although the net reproductive rate is an important statistic, we usually want to know the growth rate per year (or some other defined period). When we compare growth rates among different types of populations, the usual currency is r , the intrinsic rate of increase, or the finite rate of increase (λ), since both are measured for a specific unit of time. The intrinsic rate of increase can be extracted from life history data using an equation developed by Euler, although some authors give credit to Lotka (see Mertz 1970, or Case 2000 for its derivation). It is most often known as the Euler equation; but in any event, it is considered to be a "characteristic equation" of demography (Dingle 1990).

$$\sum l_x m_x e^{-rx} = 1 \quad (4.9)$$

This equation is useful because it allows us to determine the intrinsic rate of increase from the life table. However, since r is an exponent in a summation, it cannot be explicitly solved for if there are more than two age classes. Values of r must be estimated and tried in the Euler equation until a value is found that satisfies it. However, Laughlin (1965) and May (1976a) showed that there exists an excellent approximation for r . Assuming a stable age distribution, the approximation is based on the following:

If G = generation time, we can write: $\frac{N_G}{N_0} = R_0$.

It is also true (Eqn. 1.8) that $\frac{N_G}{N_0} = e^{rG}$.

Therefore, we can set $R_0 = e^{rG}$.

Taking natural logs of both sides of the equation gives us $\ln R_0 = rG$ and therefore:

$$r = \frac{\ln R_0}{G} \quad (4.10)$$

This tells us that the intrinsic rate of increase can be found by dividing the natural log of the increase per generation by the generation time. We now have an approximation for r , but we must calculate G , the mean generation time. Mean generation time is actually a somewhat slippery concept, and can be defined in various ways. Here we will use the definition, **the mean age of the mothers at the time of their daughter's birth**. This is the same definition as, "the average interval between reproductive onset in two successive generations" (Dingle 1990). Generation time is estimated according to the following equations, in which the age, x , is weighted by its realized fecundity, $l_x m_x$. In the second equation, discrete age intervals are used:

These equations, however, do not account for the number of individuals on the right side of the equation must be equal to the left side. Equation 4.12 in estimating r .

Once we have approximated r , we can use it to estimate the number of individuals. Note that all approximations are based on the Euler equation! Since Equation 4.12 is an approximation, the approximation adjusted for the approximation adjusted and confirmed is illustrated.

4.7 Age structure and

In the next sections, we will discuss the distribution of a population. The age distribution of a population is the proportion of a population belonging to various age categories. The age distribution belonging to a given age category is the proportion of the total population belonging to that age category.

c_x is the proportion of the total population consisting of individuals in age category x .

Whenever survivors converge on a particular age structure, a unique age structure is achieved, the age structure of the population. The age structure of a population is the proportion of the population in each age category. The age structure of a population has a stable age structure if the age structure remains constant over time. The age structure of a population has a stable age structure if the age structure remains constant over time. The age structure of a population has a stable age structure if the age structure remains constant over time.

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(4.8)

$$G = \int x l_x m_x d_x \quad (4.11a)$$

$$G = \sum x l_x m_x \quad (4.11b)$$

These equations, however, can only be used if the population is not growing. In order to account for the number of offspring being produced per individual female, the right side of the equation must be divided by the net reproductive rate, R_0 . Therefore we use Equation 4.12 in estimating G :

$$G = \frac{\sum x l_x m_x}{R_0} \quad (4.12)$$

Once we have approximated the value of G , r can be estimated using Equation 4.10. Note that all approximations of r gained using Equation 4.10 must be verified by the Euler equation! Since Equation 4.10 simply approximates r , the value of r must be verified, or the approximation adjusted using Equation 4.9, the Euler equation. The way r is estimated and confirmed is illustrated in Example 4.1.

(4.9)

4.7 Age structure and the stable age distribution

In the next sections, we are ready to begin examining the interactions between the age distribution of a population and its life table. As stated previously, the actual age distribution of a population has potentially dramatic effects on population growth in the short term. The age distribution of a population is defined as the proportions of the population belonging to various age categories at a given point in time. The proportion belonging to a given age category, x , is calculated by dividing the number of individuals in that age category by the total population size, N , producing c_x :

$$c_x = \frac{n_x}{N} = \frac{n_x}{\sum n_x} \quad (4.13)$$

c_x is the proportion of the population belonging to an age category, x , and n_x equals the number of individuals in that age category.

Whenever survivorship and fertility remain constant for long enough, a population will converge on a particular age distribution, known as the **stable age distribution**, which is unique for each combination of survivorship and fertility. Once this stable age distribution is achieved, the age distribution no longer changes unless and until survivorship or fertility change in the life table. Furthermore, the population will grow or decline at the steady rate, λ (unless the r -value = 0, in which case the population is unchanging and $\lambda = 1$), and each age class will change at the same rate as the population as a whole. If a population has a stable age distribution, λ is easy to calculate, since $N_{t+1}/N_t = \lambda$. Since $r = \ln \lambda$ (Eqn. 1.13), it is also simple to calculate r .

The stable age distribution itself can be calculated from the survivorship column of the life table. In order to predict the stable age distribution, however, it is also necessary to know the value of r as well as the survivorship function, l_x . Since the Euler equation requires

(4.10)

the knowledge of fertility (m_x), we actually must know both survivorship and fertility. The formula for predicting the stable age distribution is as follows:

$$c_x = \frac{e^{-rx}l_x}{\sum e^{-rx}l_x} \tag{4.14}$$

4.8 Projecting population growth in age-structured populations

Examine Table 4.5. The basic information on survivorship and fertility by age class would have been gathered through fieldwork. In order to project population growth into the future, we also must know the actual number of individuals belonging to each age class, again based on data we have obtained in the field. Once these data are available we can do a year-by-year projection not only of the population size as a whole, but also of the expected number of individuals in each age class. We must assume, however, that the survivorship and fertility functions do not change.

In Table 4.6 we have done some basic calculations that will tell us generally what to expect from this population. The net reproductive rate tells us that we expect this population to grow every generation ($R_0 > 1$). In the ensuing projection we will need the age-specific probability of surviving to the next age class (p_x); accordingly we have devoted a

Table 4.5 Hypothetical life table for a population. This table will be used to illustrate a simple population projection (Table 4.6).

Age, x	l_x	m_x	p_x	q_x	$l_x m_x$
0	1.00	0	0.50	0.50	0
1	0.50	2.0	0.40	0.60	1.0
2	0.20	1.0	0.50	0.50	0.2
3	0.10	1.0	0	1.00	0.1
4	0	0	-	-	-
Sums		GRR = 4.0			$R_0 = 1.3$

Table 4.6 Projected population growth based on life history from Table 4.5 and starting with 200 individuals in age class zero (newborn).

Age, x	n_x at $t = 0$	c_x at $t = 0$	n_x at $t = 1$	c_x at $t = 1$	n_x at $t = 2$	c_x at $t = 2$	n_x at $t = 3$	c_x at $t = 3$	Calculated stable age distribution
0	200	1.00	200	0.67	240	0.63	300	0.625	0.625
1	0	0	100	0.33	100	0.26	120	0.250	0.258
2	0	0	0	0	40	0.11	40	0.083	0.082
3	0	0	0	0	0	0	20	0.042	0.035
4	0	0	0	0	0	0	0	0	0
Sums	200	1.00	300	1.00	380	1.00	480	1.00	1.00

column in Table 4.5 dying in the next age

We begin this projection with newborn females at time $t = 0$ on that assumption (Table 4.5). The population in that age category at time $t = 0$ of the non-zero age class is the appropriate age category for the one-year-old individuals at time $t = 0$ by p_0 . The number of one-year-old females at time $t = 0$ of one-year-old females is p_0 . Since we lack one-year-old females, two-, three-, or four-year-old females.

To find the number of one-year-old females values by the number of newborn females, the number of newborn females by the appropriate m_x value. In Table 4.5, m_1 has 2.0 female offspring at $t = 1$. The total population at time $t = 1$ is 300. To find the number of one-year-old females, we lined above, giving 200 by multiplying p_1 by the number of newborn individuals. The number of one-year-old females by the number of newborn individuals for $t = 3$. The last column in Table 4.6, Equation 4.14. Notice that the population have moved to with age class zero at time $t = 0$ with 200 individuals. In the above example, the population periods t to $t + 1$ are:

λ from $t = 0$ to $t = 1$
 λ from $t = 1$ to $t = 2$
 λ from $t = 2$ to $t = 3$
 λ from $t = 3$ to $t = 4$

Notice how quickly the population size is increasing. The stable age distribution is 0.206 and 0.258. Exercises like this show that the population is heavily influenced by the generation time and the increase is influenced by the life history.

In Example 4.1, we do that, test your understanding of the intrinsic rate of

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$l_x m_x$
0
1.0
0.2
0.1
-
$R_0 = 1.3$

ble 4.5 and

t	Calculated stable age distribution
3	
5	0.625
0	0.258
3	0.082
2	0.035
	0
	1.00

column in Table 4.5 to p_x as well as to its opposite (q_x), the age-specific probability of dying in the next age class. The last column allows us to calculate R_0 .

We begin this projection by assuming that we have founded this population with 200 newborn females at time $t = 0$ (Table 4.6). We have completed the first two columns based on that assumption (n_x = the number in an age category, c_x = the proportion of the population in that age category). To project the population, the number of individuals in each of the non-zero age categories is found by multiplying the number of individuals in the appropriate age category by the suitable p_x value. For example, to find the number of one-year-old individuals at time $t = 1$, we multiply the number of newborn individuals at time $t = 0$ by p_0 . The number of two-year-olds at time $t = 1$ is found by multiplying the number of one-year-olds at time $t = 0$ by p_1 , and so on. In this case, to find the number of one-year-old females at time $t = 1$, we simply multiply 200 by p_0 (0.50), giving us 100. Since we lack one-, two-, or three-year-old individuals at time $t = 0$, there can be no two-, three-, or four-year-old individuals at time $t = 1$.

To find the number of newborn individuals at time $t = 1$, multiply the appropriate m_x values by the number of individuals in each age class at time $t = 1$. In this example, to find the number of newborn individuals we multiply the number of one-year-olds by the appropriate m_x value. In this case, $m_1 = 2.0$; that is, each of the 100 females that has survived has 2.0 female offspring, on average. Therefore there are 200 newborn females at time $t = 1$. The total population is 300 and our c_x values are based on that number (Table 4.6). To find the number of one-year-old females at time $t = 2$, we repeat the procedure outlined above, giving us 100 again. The number of two-year-old females at time $t = 2$ is found by multiplying p_1 (0.40) by 100, giving us 40 two-year-old individuals. The number of newborn individuals is found by multiplying 100 one-year-old females by 2.0 and 40 two year old females by 1.0. That is, multiply by the appropriate m_x values. The number of newborn individuals is therefore 240 and the total population is 380. Confirm the values for $t = 3$. The last column in Table 4.6 is the calculated **stable age distribution**, based on Equation 4.14. Notice that after only three time periods the population proportions (c_x) have moved to within a few tenths of the stable age distribution, even though we started at time $t = 0$ with only one age class (200, $x = 0$).

In the above exercise, the finite rate of increase can be calculated for each of the time periods t to $t + 1$ as N_{t+1}/N_t . The results are as follows:

- λ from $t = 0$ to $t = 1$: $300/200 = 1.50$
- λ from $t = 1$ to $t = 2$: $380/300 = 1.27$
- λ from $t = 2$ to $t = 3$: $480/380 = 1.26$
- λ from $t = 3$ to $t = 4$: $586/480 = 1.22$

Notice how quickly λ moves to 1.22. The calculated r from the Euler equation for this life table is 0.206 and therefore the predicted value of λ at the stable age (e') distribution is 1.23. Exercises like this show us three things: (i) in the short term the growth of a population is heavily influenced by its age distribution; (ii) nevertheless, a population with a short generation time can move rapidly to its stable age distribution; and (iii) the finite rate of increase is influenced by the actual age distribution, but it settles in at the predicted value from the life history table ($= e'$) as the population reaches the stable age distribution.

In Example 4.1, find the necessary information to project the population. As you do that, test yourself to see if you understand how to calculate generation time, G , the intrinsic rate of increase, and the stable age distribution (SAD) from the life history table.

Example 4.1

Find GRR, R_0 , and G . Estimate r and then find its true value with the Euler equation. Verify the predicted stable age distribution (SAD). Project this population as described above. After reading the next section, use the Leslie matrix to project the population.

Age	l_x	m_x	p_x	q_x	$l_x \times m_x$	$x \times l_x \times m_x$	Euler based on $r = 0.152$	Euler based on $r = 0.154$	$l_x \times e^{-rx}$	c_x of SAD
0	1.00	0	0.250	0.750	0.00	0.00	0	0	1.000	0.733
1	0.25	0	0.400	0.600	0.00	0.00	0	0	0.214	0.157
2	0.10	7.0	0.800	0.200	0.70	1.40	0.517	0.514	0.073	0.054
3	0.08	7.5	0.500	0.500	0.60	1.80	0.380	0.378	0.050	0.037
4	0.04	5.0	0.250	0.750	0.20	0.80	0.109	0.108	0.022	0.016
5	0.01	0	0.000	1.000	0.00	0	0	0	0.005	0.003
6	0	0	-	-	0.00	0	0	0	0.000	0.000
Σ		GRR = 19.5			$R_0 = 1.50$	4.00	1.006	1.000	1.364	1.000
							Estimated value of $r = 0.152$		Predicted value of $\lambda = e^r$ $= 1.17$	

Population projection

Age	n_x at $t = 0$	c_x at $t = 0$	n_x at $t = 1$	c_x at $t = 1$	n_x at $t = 2$	c_x at $t = 2$	n_x at $t = 3$	c_x at $t = 3$	n_x at $t = 4$	c_x at $t = 4$
0	250	0.714	318	0.743	359	0.729	420.6	0.733	492.10	0.733
1	60	0.171	62.5	0.146	79.5	0.162	89.75	0.156	105.15	0.157
2	20	0.057	24	0.056	25	0.051	31.8	0.055	35.90	0.054
3	12	0.034	16	0.037	19.2	0.039	20	0.035	25.44	0.038
4	6	0.017	6	0.014	8	0.016	9.6	0.017	10.00	0.015
5	2	0.006	1.5	0.004	1.5	0.003	2	0.003	2.40	0.003
6	0	0.000	0	0.000	0	0.000	0	0.000	0	0
$N = 350$		1.000	$N = 428$	1.000	$N = 492.2$	1.000	$N = 573.75$	1.000	$N = 670.99$	1.000
$\lambda =$ 428/350 = 1.22				$\lambda =$ 492/428 = 1.15		$\lambda =$ 574/492 = 1.17		$\lambda =$ 671/574 = 1.17		

4.9 The Leslie or population projection matrix

This process of projecting the population one age class and one year at a time, as done above, is time-consuming and tedious. Leslie (1945) showed that populations could easily be projected through the use of matrix algebra. If you are not familiar with matrix

Table 4.7 General for one time period

Age class	
0	
1	
2	
3	
4	

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For age class 1 the nu
For age class 2 the nu
For age class 3 the nu
For age class 4 the nu

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Table 4.7 General matrix format for projecting a population with five age classes for one time period ($t = 0$ to $t = 1$).

Age classes		Matrix					$t = 0$	$t = 1$
0		p_0m_1	p_1m_2	p_2m_3	p_3m_4	0	n_0	n_0
1		p_0	0	0	0	0	n_1	n_1
2		0	p_1	0	0	0	n_2	n_2
3		0	0	p_2	0	0	n_3	n_3
4		0	0	0	p_3	0	n_4	n_4

For age class 0 the number of individuals is based on: $p_0m_1n_0 + p_1m_2n_1 + p_2m_3n_2 + p_3m_4n_3 + 0$.
For age class 1 the number of individuals is calculated as: $p_0n_0 + 0 + 0 + 0 + 0$.
For age class 2 the number of individuals is calculated as: $0 + p_1n_1 + 0 + 0 + 0$.
For age class 3 the number of individuals is calculated as: $0 + 0 + p_2n_2 + 0 + 0$.
For age class 4 the number of individuals is calculated as: $0 + 0 + 0 + p_3n_3 + 0$.

algebra see the primer in Appendix 2. The matrix approach allows quick calculations of changes in the age structure and total population size as well as a quick method for finding λ when there is a stable age distribution. The survivorship and fertility columns are placed in matrix form $|A|$. The population itself is considered a column vector which, when multiplied by the matrix, produces a new column vector representing the population at time $t + 1$:

$$N_{t+1} = |A|N_t \tag{4.15}$$

The format for the matrix is as shown in Table 4.7. The p_x values (the probabilities of surviving from age x to age $x + 1$) appear in the matrix in the off diagonal. The first row consists of the products $p_x \times m_{x+1}$. The matrix must be a square matrix, with the final column consisting of zeros. In this example, with five age classes, we have a 5×5 matrix. Given the rules of matrix multiplication, the product of the matrix times the column vector (representing the population by age classes at $t = 0$) results in a column vector at time $t = 1$.

If we use the life table from Table 4.5, the resultant matrix is as shown in Table 4.8. If we then multiply this matrix by the column vector for time $t = 2$ from Table 4.6, we can calculate the column vector for time $t = 3$. The result is identical to the projection we did above in Table 4.6.

4.10 A second version of the Leslie matrix

To this point, in constructing our life tables we have assumed that the year begins with the reproductive season. For example, if we are developing a life table for white-crowned sparrows we might assess the number of eggs that have hatched and assign the hatchlings to age class zero. However, in some studies this approach is not practical and the study begins with counts of animals that have completed at least one year of life. The count is done before the production of newborn individuals, but there is no count of the number of newborn individuals. Assume it is possible, however, to estimate both fertility and

Table 4.8 Matrix projection based on life-history data found in Table 4.5. Column vectors are based on time periods $t = 2$ and $t = 3$ in Table 4.6

Age classes		Matrix			Column vectors		
					$t = 2$	$t = 3$	
0	$0.5 \times 2 = 1.0$	$0.4 \times 1 = 0.4$	$0.5 \times 1 = 0.5$	0	240	300	
1	0.5	0	0	0	100	120	
2	0	0.4	0	0	40	40	
3	0	0	0.5	0	0	20	
Total	0	0	0	0	380	480	

Age, x	Calculations for column vector, time $t = 3$	Resultant column vector for time $t = 3$
0	$(1.0 \times 240) + (0.40 \times 100) + (0.50 \times 40)$	300
1	0.50×240	120
2	0.40×100	40
3	0.50×40	20
Total		480

survivorship for age classes from year 1 onward. For example, see Table 4.9, which is based on Table 4.5. The life table simply begins with age class 1. Note that in this version of the matrix all of the fertility values in the first row are simply multiplied by p_0 , since in order to find the number of one-year-old individuals we are multiplying the total number of newborn by the probability of surviving to age class 1.

We end up with the same result by either method, but we do not have exact data on age class zero in this second method. Interestingly enough, since age-class-zero individuals do not reproduce, the identical finite rate of increase (λ) can be derived from either method. And since the second method requires a smaller matrix, calculations can be vastly simplified, as shown in the next section.

Table 4.9 A population projection matrix, based on Table 4.5, in which the year begins prior to reproduction and no count is made of the zero-year age class. The population is projected from time $t = 2$ to 3 as in Section 4.9.

				$t = 2$	$t = 3$					$t = 2$	$t = 3$
$m_1 p_0$	$m_2 p_0$	$m_3 p_0$	$m_4 p_0$	n_1	n_1	1.0	0.5	0.5	0	100	120
p_1	0	0	0	n_2	n_2	0.4	0	0	0	40	40
0	p_2	0	0	n_3	n_3	0	0.5	0	0	0	20
0	0	p_3	0	n_4	n_4	0	0	0	0	0	0

Table 4.10 Simplified life

Age or stage class

Y = young adult
A = mature adult

4.11 The Lefkovitch m

Lefkovitch (1965) noticed that the functions remain relative to the age he proposed using "stage" instead of age, etc. Recall our discussion of the method for plant populations. For the Carolina gray squirrel population, the gray squirrel life table shows that this we have eliminated the need for p_A (adult survivorship) of life as $p_Y = 0.25$.

Lefkovitch showed that by setting up the projection matrix with many of the age classes in the same stage class, the number that survives is placed in the (mature adult survivorship) of this 2×2 matrix.

Using $Y =$ "young adult" and $A =$ "mature adult" can be simplified as follows:

$$\begin{bmatrix} m_Y p_0 \\ p_A \end{bmatrix}$$

Let us now project the population of 50 "young adults" at time t to time $t + 1$.
$$\lambda = \frac{N_{t+1}}{N_t} = 1.28 \text{ (180)}$$

Table 4.11 Projected population matrix.

Stage class	
Y	0.25
A	0.80

Table 4.10 Simplified life table for the gray squirrel.

Age or stage class	m_x	p_x
Y = young adult	1.28	0.25
A = mature adult	2.28	0.80

4.11 The Lefkovitch modification of the Leslie matrix

Lefkovitch (1965) noticed that for many organisms the yearly fertility and survivorship functions remain relatively constant once adulthood is reached. Instead of specific age classes, he proposed using "stage classes" based on life stages such as juvenile, young adult, adult, etc. Recall our discussion in the first part of this chapter of the necessity to use such a method for plant populations. Now review Table 4.3 in section 4.3 above for the North Carolina gray squirrel population. Notice that by using method two (Section 4.10 above) the gray squirrel life table can be simplified to two stages as shown in Table 4.10. To do this we have eliminated some of the variability in year-to-year adult survivorship, using 0.80 for p_A (adult survivorship). Further, we have estimated survivorship in the first year of life as $p_Y = 0.25$.

Lefkovitch showed that in spite of this lumping the growth rate λ is conserved. In setting up the projection matrix based on this lumping, we must realize that adults from many of the age classes that we have placed together are simply recycled back into the same stage class from which they came for many years. That is, a three-year-old that survives is placed back in the "mature adult" stage class. Therefore, when placing p_A (mature adult survivorship) into the matrix, it ends up in the bottom right-hand corner of this 2×2 matrix.

Using Y = "young adult" and A = "Mature adult" stages, the gray squirrel matrix can be simplified as follows:

$$\begin{vmatrix} m_Y p_0 & m_A p_0 \\ p_A & p_A \end{vmatrix} = \begin{vmatrix} 1.28 \times 0.25 & 2.28 \times 0.25 \\ 0.80 & 0.80 \end{vmatrix} = \begin{vmatrix} 0.325 & 0.57 \\ 0.80 & 0.80 \end{vmatrix}$$

Let us now project this population and determine its growth rate, λ . We will start with 50 "young adults" and 90 "mature adults" (Table 4.11). The yearly calculated value of $\lambda = \frac{N_{t+1}}{N_t} = 1.28$ (180/140, 230/180, 294/230, etc.). By contrast, if you were to use all eight

Table 4.11 Projection of the gray squirrel population using the 2×2 simplified matrix.

Stage class	Matrix	$t = 0$	$t = 1$	$t = 2$	$t = 3$
Y	0.325 0.570	50	68	86	110
A	0.80 0.80	90	112	144	184
		$\Sigma = 140$	$\Sigma = 180$	$\Sigma = 230$	$\Sigma = 294$

age classes, including age class zero, the λ -value turns out to be 1.26 (you can prove this to yourself using Table 4.3 and projecting the population). Given that we assumed one p_x for all adult age classes, and given the uncertainties of actual survivorship and fertility data we might gather in the field, these two estimates of the finite rate of increase are adequately close. As Lefkovitch (1965) emphasized, the reduced matrix has the same λ as its larger counterpart using all age classes.

4.12 Dominant latent roots and the characteristic equation

Following the rules of matrix multiplication, if the matrix does not change (meaning that l_x and m_x remain constant), we can write:

$$N_1 = |A|N_0$$

$$N_2 = |A|N_1 = |A||A|N_0$$

$$N_3 = |A|N_2 = |A||A||A|N_0$$

This generalizes to:

$$N_t = |A|^t N_0 \quad (4.16)$$

Therefore a population can be projected to any time in the future. We can also project a population backwards in time. The advantage of this is that we can examine properties a population might have had in the past, assuming the present life table. The backwards projection requires the "identity matrix." The identity matrix is equivalent to the number one in algebra and is such that one can write the following:

$$I|A| = |A|I = |A| \quad (4.17)$$

Each number has an inverse in algebra (except zero) such that $(x) \times (1/x) = 1$. The inverse of a matrix is such that $|A||A|^{-1} = I$ (the identity matrix). If the inverse of $|A|$ is $|B|$ then $|A||B| = I$.

For example, if $|A| = \begin{vmatrix} 2 & 5 \\ 3 & 8 \end{vmatrix}$, then $|B| = \begin{vmatrix} 8 & -5 \\ -3 & 2 \end{vmatrix}$. The result of multiplying $|A||B|$ is the two-by-two identity matrix: $\begin{vmatrix} 1 & 0 \\ 0 & 1 \end{vmatrix}$ (See Appendix 2).

The inverse of a matrix only exists when the matrix is square and when the matrix has a "determinant." A determinant for a square matrix is a particular scalar number (see Appendix 2) that is easy to calculate for a 2×2 matrix, but becomes increasingly complicated for larger matrices. The projection matrix has an inverse if $|A||B| = I$. We can then use $|B|$ to project the matrix backwards from time $t = 0$ to $t = -1, -2, -3$, etc:

$$N_t = |B|^t N_0 \quad (4.18)$$

This allows us to compare the actual population of 1955, for example, with the potential population in that year, based on present-day survivorship and fertility values.

As discussed earlier, w grows as the same rate as λ . Thus: $n_{x(t+1)} = n_{x(t)}\lambda$ for

Since $N_{t+1} = |A|N_t = \lambda N_t$

Zero is a column vector

Equation 4.19a is known as the characteristic equation. It is a square matrix, and λ is the value of the characteristic equation. The characteristic equation of a n -by- n matrix is of the form $\lambda^n - a_{11}\lambda^{n-1} + \dots + (-1)^{n+1}a_{nn} = 0$ and has n solutions. But the dominant latent root). This determinant can be used to

As explained in detail, the determinant of the expression projecting the matrix

For more information, see the book. For a 2×2 matrix, we

Now we subtract the determinant, yielding:

The determinant of the cross products, resulting in

$$(a_{11} - \lambda)$$

Solving for λ looks extremely tedious (1965), many matrices

Now let's return to the previous section:

As discussed earlier, when a population has a stable age distribution, each age group grows at the same rate as the population as a whole; that is, at the finite rate of increase, λ . Thus: $n_{x(t+1)} = n_{x(t)}\lambda$ for all age classes (x). And $N_{t+1} = N_t\lambda$. In matrix form, we have:

$$N_{t+1} = \lambda N_t = \lambda(I N_t) = \lambda I(N_t)$$

Since $N_{t+1} = |A|N_t = \lambda I N_t$, we can write:

$$|A| - \lambda I = 0 \quad (4.19a)$$

Zero is a column vector consisting of all zeros.

Equation 4.19a is known as the **characteristic equation** for a matrix. It only exists for square matrices, and λ is known as the "latent root," "the characteristic root" or the **Eigenvalue** of the characteristic equation. When the matrix $|A|$ is of the order n (that is, a four-by-four matrix is of the order 4), the characteristic equation is a polynomial of degree n , and has n solutions. But for the Leslie matrix, there is only one positive root (or **dominant latent root**). This dominant latent root $= \lambda$ and Leslie has shown that $\lambda = e^r$. Thus matrix algebra can be used to solve for r from basic life history data.

As explained in detail by Case (2000), one way of solving for λ is to find the determinant of the expression $|A| - \lambda I$ and setting it equal to zero. In other words, instead of projecting the matrix to find λ as we did above, we can find λ if we solve the expression:

$$\det(|A| - \lambda I) = 0 \quad (4.19b)$$

For more information on determinants and basic matrix operations, see Appendix 2. For a 2×2 matrix, we start by multiplying λ by the identity matrix, giving us:

$$\begin{vmatrix} 1 & 0 \\ 0 & 1 \end{vmatrix} \times \lambda = \begin{vmatrix} \lambda & 0 \\ 0 & \lambda \end{vmatrix}$$

Now we subtract this from our 2×2 matrix (see rules of subtraction, Appendix 2), yielding:

$$\begin{vmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{vmatrix} - \begin{vmatrix} \lambda & 0 \\ 0 & \lambda \end{vmatrix} = \begin{vmatrix} a_{11} - \lambda & a_{12} \\ a_{21} & a_{22} - \lambda \end{vmatrix}$$

The determinant of a simple 2×2 matrix is found by taking the difference between the cross products, resulting in the following:

$$(a_{11} - \lambda)(a_{22} - \lambda) - (a_{21})(a_{12}) = \lambda^2 - \lambda(a_{11} + a_{22}) + (a_{11}a_{22}) - (a_{21}a_{12}) = 0 \quad (4.20)$$

Solving for λ looks difficult, and finding the determinant for more complex matrices is extremely tedious without computer software. As discussed above, thanks to Lefkovitch (1965), many matrices can be simplified to this 2×2 form.

Now let's return to the 2×2 matrix for the gray squirrel population we found in the previous section:

$$\begin{vmatrix} 0.325 & 0.57 \\ 0.80 & 0.80 \end{vmatrix}$$

Solving for λ using the method outlined above (Eqn. 4.20) we have:

$$(0.325 - \lambda)(0.80 - \lambda) - (0.80 \times 0.57) = 0.$$

This gives us:

$$\lambda^2 - 1.125\lambda + 0.26 - 0.456 = \lambda^2 - 1.125\lambda - 0.196 = 0$$

We can solve this equation using the formula for the solution of a quadratic equation ($ax^2 + bx + c = 0$, recall your high school algebra!):

$$\lambda = \frac{-b \pm \sqrt{b^2 - 4ac}}{2a}$$

$$\lambda = \left(1.125 \pm \sqrt{1.266 + 0.784}\right) / 2 = \frac{1.125 \pm 1.432}{2} = 1.28$$

Although there is another solution, the positive or dominant root for λ is 1.28, which is the same value we found above by projecting population growth and finding λ after evaluating N_{t+1}/N_t .

4.13 Reproductive value

As biologists and conservation biologists evaluate life histories, they are often interested in which age classes contribute most heavily to present and/or future population growth. For this analysis they calculate a parameter known as the reproductive value. One application of the reproductive value focuses on whether natural selection can regulate events late in the life span of an organism when reproductive value is very low. Behavioral biologists have suggested that in dominance hierarchies, individuals with the greatest reproductive potential or value will be supported by their mothers or others in the population (Alberts and Altmann 2003). Conservation biologists attempting to evaluate what intervention strategy will give them the biggest bang for their buck (in terms of long-term survival of the population) may use reproductive value in determining which age classes are likely to produce the desired increase in growth rate.

To evaluate reproductive potential, simply examining the fertility column is usually misleading. For example, if one-year-old females have, on average, two female offspring, but two-year-old females have four female offspring, one might conclude that the two-year-old individuals contribute more to population growth. However, suppose that the survivorship value for $l_1 = 0.1$ and for $l_2 = 0.01$. The products of $l_x m_x$ tell us that one-year-old females produce 0.2 females and two-year-olds only 0.04 females per generation. Evidently an evaluation of reproductive potential of a given age class must take into account both survivorship and fertility. Furthermore, the value of a given female depends not on

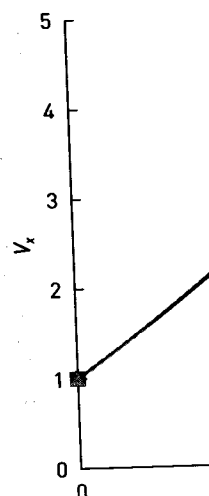


Figure 4.12 The

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Figure 4.12 Three methods of computing reproductive value.

just her present reproduction, but the potential for future reproduction. For example, in many species females become more fecund and more adept at successfully raising offspring as they mature, leading to an increase in m_x with age, followed by a decrease as they senesce. On the other hand, in mammals that suckle their young for more than a year, reproductive rates may be suppressed in the year following a birth, leading to oscillations in birth rates by age class across the population. For example, in Amboseli baboons $m_{10} = 0.816$, $m_{11} = 0.649$, $m_{12} = 0.818$, and $m_{13} = 0.554$ (Alberts and Altmann 2003).

Reproductive value is a number that measures the relative reproductive potential of an individual of a given age. It can also be thought of as the weighted average of present and future reproduction by a female or male of age x . It is the relative value of a daughter born i time-units in the future when the population size will be N_{t+i} . Reproductive value is scaled so that the value for the first age class equals 1.0 (Fig. 4.12). There are several different ways of computing reproductive value (Lanciani 1998). In Example 4.2 I present the traditional equation for reproductive value as method one (Lanciani 1998). A second method produces reproductive values that are closer to the original concept of R.A. Fisher (1930) and to that derived from the matrix-algebra approach (Caswell 1989). Conceptually, the second value is defined as "the present value of future offspring" of a female of age x , and ignores reproduction by the present age class (method two). In other words, values from age $x + 1$ to the end of life are used. Reproductive value can also be found in the Populus computer simulations developed by University of Minnesota ecologist Don Alstad (2001). In method one, as in Populus, values from age x to the end of life are used.

The differences between the two approaches can be gleaned by working through Example 4.2. In the formula for reproductive value, the survivorship functions l_x , m_x , and r are as usual. In Equation 4.21, the numerator is simply the Euler equation. In method two the summation is from the age $x + 1$ to the end of life. The summation in the numerator is from the age class in question (x) to the end of the life span (z).

$$V_x = \frac{\sum_x^z e^{-rx} l_x m_x}{e^{-rx} l_x} \tag{4.21}$$

Sample calculations are found in Example 4.2. Note that you should be able to confirm that $r = 0.371$ and $\lambda = 1.449$, assuming a stable age distribution.

Example 4.2

To calculate reproductive value, we need the following information:

Age, x	l_x	m_x	$e^{-rx} \times l_x \times m_x$	$e^{-rx} \times l_x$
0	1.00	0	0	1.000
1	0.60	0	0	0.414
2	0.50	3.0	0.714	0.238
3	0.40	2.0	0.263	0.132
4	0.10	1.0	0.023	0.023
5	0	0	0	0
Sum			1.000	

Calculation of reproductive value, V_x :

Age, x	Method one	Method two
0	$(0 + 0 + 0.714 + 0.263 + 0.023)/1.000 = 1.000$	$(0 + 0.714 + 0.263 + 0.023)/1.000 = 1.000$
1	$(0 + 0.714 + 0.263 + 0.023)/0.414 = 2.42$	$(0.714 + 0.263 + 0.023)/0.414 = 2.42$
2	$(0.714 + 0.263 + 0.023)/0.238 = 4.20$	$(0.263 + 0.023)/0.238 = 1.20$
3	$(0.263 + 0.023)/0.132 = 2.17$	$0.023/0.132 = 0.17$
4	$0.023/0.023 = 1.000$	$0/0.023 = 0$

All methods produce the typical triangular shape when reproductive value, V_x , is graphed against age (Fig. 4.12). See Fig. 4.8 of Alberts and Altmann (2003) for an example of triangular reproductive values of male and female Amboseli baboons. If you run Populus and bring up reproductive value for this life table it produces a hybrid. The values for method 1 are identical for ages 0–3. However, instead of assigning a value of 1.00 to the last age class, it drops it to zero, as in method 2.

4.14 Conclusions:

We have learned that plant and animal fertility differ greatly and display many variations. The schedule is most sensitive to conservation growth. Thus the we can make predictions for endangered populations survivorship and in a position to be effective in promoting

For example, et al. (1997) on a from Morris and ing or declining long-term growth format from Section is 0.989.

We now ask, particular demographic survivorship on above matrix, with both hatchlings for two-year-olds summarizes the has the greatest tually no effect population growth on our conclusions our estimate decrease. A lead us to be

Table 4.12 S [Schmutz et al.]

Survival of hatchlings =

0.136

(4.21)

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n:

$e^{-rx} \times l_x$

- 1.000
- 0.414
- 0.238
- 0.132
- 0.023
- 0

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4.14 Conclusions: sensitivity analysis

We have learned that age- or stage-structured growth is common in most plant and animal populations, but the details of both survivorship and fertility differ greatly across species. For example, natural populations display many variations in survivorship, although a type III survivorship schedule is most common. Most of the "charismatic megafauna" of interest to conservation biologists and the general public shows age structured growth. Thus the techniques outlined in this chapter are necessary before we can make predictions about the potential for growth and recovery of an endangered population. We must understand the effects that age-specific survivorship and fertility have on the behavior of a population before we are in a position to implement a management plan that would actually be effective in promoting its long-term survival.

For example, examine Table 4.12. These data were gathered by Schmutz *et al.* (1997) on a population of the emperor goose (*Chen canagica*) (analysis from Morris and Doak 2002). Given this information, is this population growing or declining? What aspects of its life history are most important to its long-term growth rate? To answer these questions, we will use the matrix format from Section 4.10. It turns out that the long-term λ for this population is 0.989.

We now ask, "How sensitive is population growth (or extinction risk) to particular demographic changes?" Specifically, will a particular change in survivorship or fertility have a large impact on the growth rate, λ ? Using the above matrix, we have substituted survivorship values from 0.136 to 1.00 for both hatchlings (S_0) and older birds (S_{2+}), and fertility rates of 0.136–2.000 for two-year-old (F_2) and three-year-old and older birds (F_{2+}). Figure 4.13 summarizes this analysis. Obviously survival, especially that of the older birds, has the greatest effect on the growth rate (λ). Increases in fertility have virtually no effect. A related point is that, since adult survival is so critical to population growth, errors in our estimates would have a very large impact on our conclusions about this population. As it stands now, from this matrix our estimate of λ is $0.989 < 1.000$, and we expect this population to slowly decrease. A small change in our estimation of survivorship, however, would lead us to believe that this population is stable or growing. For example, a

Table 4.12 Survivorship and fertility of an emperor goose population [Schmutz *et al.* 1997].

Survival of hatchlings = S_0	Survival of one-year-old and birds = S_{2+}	Fertility of two-year-old birds = F_2	Fertility of three-year-old and older birds = F_{2+}
0.136	0.893	0.639	0.894

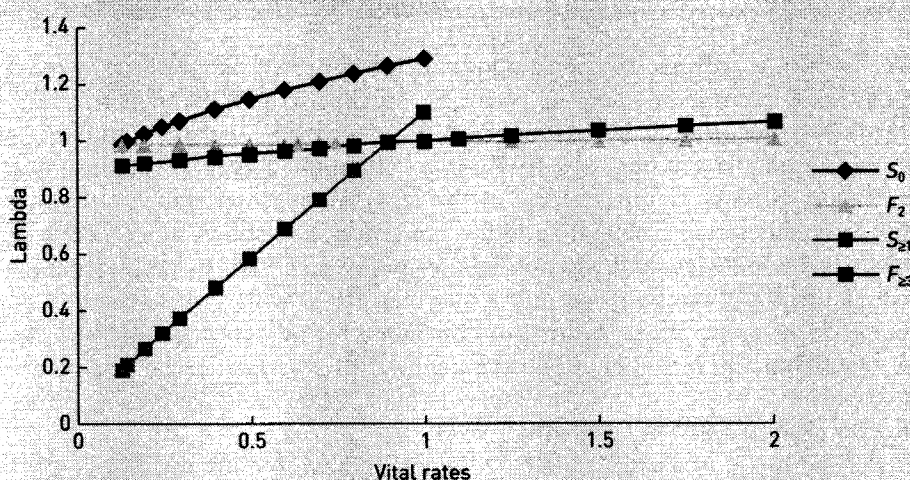


Figure 4.13 The effect of changing vital rates on the value of lambda in an emperor goose (*Chen canagica*) population. An increase in survivorship of adults (one-year-old and older birds) has the greatest effect. Increases in fertility have a negligible effect on λ .

change in adult survival from 0.893 to 0.905 changes lambda from 0.989 to 1.001. A change in juvenile survivorship from 0.136 to 0.155 changes the expected lambda to 1.000.

An examination of this sort is known as a perturbation or "sensitivity analysis." Although Fig. 4.13 is convincing, conservation biologists have sought to summarize the kind of analysis we have done above into a single number that would summarize the sensitivity of lambda to particular vital rates. The most common basic measure of sensitivity is the slope of the tangent taken on the curve of lambda as a function of each vital rate. Problems with this approach include the possibility of nonlinearity in the relationship between lambda and a particular vital (survivorship or fertility) rate. A second issue is the scaling of sensitivity values. Obviously survivorship scales on a strict 0.0–1.0 scale, while reproduction can scale to very large numbers (number of acorns produced by an oak tree). These comparisons can be made more meaningful by examining the proportional change in lambda as a proportion of change in the vital rates. These calculations result in a measure known as **elasticity**. Elasticity, then, is a standardized sensitivity that measures the effects of proportional changes in vital rates. That is, elasticities tell us the effect of perturbations in vital rates that are all of the same relative magnitude. Elasticities are standardized to sum to 100%.

For the emperor goose population discussed above the vast majority (92% of elasticity) of sensitivity was in the survival of the one-year-old and older birds (Morris and Doak 2002). An analysis of the Amboseli baboon

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population by Alberts and Altmann (2003) led to similar conclusions. That is, fertility represented just 9% of the total elasticity for both males and females. Survival of the pre-reproductive age classes accounted for 37% of the total elasticity for females and 62% for males. Details on the calculation of both sensitivity and elasticity values can be found in Morris and Doak (2002) or Alberts and Altmann (2003).

What should be done to promote the long-term survival of these two populations, or of other populations described in the first paragraph of this chapter? What evolutionary forces have led to a particular life history in the first place? These are just two of many questions for which there are no easy answers. Still, the analyses outlined in this chapter should have given you the tools necessary to at least begin to address these issues.