

# Life Tables and Demography

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**T**he Dall mountain sheep, *Ovis dalli*, lives in mountainous regions, including the Arctic and sub-Arctic regions of Alaska. In the late 1930s, the U.S. National Park Service was bombarded with public concerns that wolves were responsible for a sharp decline in the population of Dall mountain sheep in Denali National Park (then Mt. McKinley National Park). Shooting the wolves was advocated as a way of increasing the number of sheep. Because meaningful data on sheep mortality were nonexistent, the Park Service enlisted biologist Adolph Murie to collect relevant information. In addition to spending many hours observing interactions between wolves and sheep, Murie also collected sheep skulls and determined the sheep's age at death by counting annual growth rings on the horns. Murie's study was one of the first attempts to systematically collect data on all life history stages of an organism.

This chapter follows Murie's lead. For a variety of organism, we examine how long individuals survive in a population and at what age they die. Such information is typically summarized in tables but can also be presented graphically. Later, we gather information about the reproductive rates of individuals of various ages in the population. When we know how long females survive and the reproductive rates of different aged females, we can make predictions about how the population will grow. In the following discussions we assume that there is no immigration or emigration into or out of the population and that any changes in population size are a result of births and deaths.

## 9.1 Age Distributions, Life Tables, and Survivorship Curves Summarize Survival Patterns

One way to determine the survival and mortality of individuals in a population is to examine a cohort of individuals from birth to death. A **cohort** is a group of same-aged young which grow and survive at similar rates. A population is often made up of organisms from a variety of different cohorts, each of different ages, so we say the population consists of different age classes. An **age class** consists of individuals of a particular age, for example, three-year-olds. For most animals and plants, monitoring a cohort involves marking a group of individuals in a population as soon as they are born or germinate and following their fate through their lifetime. Researchers use this information to construct a life table. A **life table** provides data on the number of individuals alive in different age classes and the age-specific survival or mortality rates in these age classes. We can also present information from life tables graphically in the form of survivorship curves. A **survivorship curve** is a graphical representation of the numbers of individuals alive in a population at various ages.

Two types of life tables exist, a cohort life table and a static life table. The **cohort life table** follows a cohort of individuals from birth to death just as we have described. Cohort life tables can be used to estimate the age-specific probabilities of survival. A **static life table** accomplishes the same goal, but instead of following a cohort of individuals from life to death, data is gathered on the age structure of a given population at one point in time. For some long-lived organisms such as tortoises, elephants, or trees, following an entire cohort from birth to death is impractical, so a snapshot approach is used. This is the approach that Adolf Murie adopted in his studies of the Dall mountain sheep.

### 9.1.1 Age distributions reflect survival and mortality patterns

Numbers of individuals in different age classes can be calculated for any time period, but they often represent one year. Males are not often included in these calculations, because they are typically not the limiting factor in population growth. For example, even if there were only a few males in the population, they could probably fertilize all the females. However, if there were only a few females, then very few young would be born and population growth would be severely slowed. We expect that a population increasing in size should have a large number of young, because individuals are reproducing at a high rate. On the other hand, a decreasing population should have few young because of limited reproduction. An imbalance in age classes can have a profound influence on a population's future. For example, in an overexploited fish population, the bigger, older reproductive age classes are often removed. If the population experiences reproductive failure for 1 or 2 years, there will be no young fish to move into the reproductive age class to replace the removed fish, and the population may collapse. Other populations experience removal of younger age classes. Where populations of white-tailed deer

are high, they overgraze the vegetation and eat many young trees, leaving only older trees, whose foliage is too high up for them to reach (**Figure 9.1**). This can have disastrous effects on the future population of trees, for while the forest might consist of healthy mature trees, when these die, there will be no replacements. Removal of deer predators such as panthers and wolves often allows deer numbers to skyrocket and survivorship of young trees in forests to plummet.

### 9.1.2 Static life tables provide a snapshot of a population's age structure from a sample at a given time

Let's examine a static life table for the North American beaver, *Castor canadensis*. Prized for their pelts, by the mid-19th century these animals had been hunted and trapped to near extinction. Beavers began to be protected by laws in the 20th century, and populations recovered in many areas, often growing to what some considered to be nuisance status. In Newfoundland, Canada, legislation supported trapping as a management technique. From 1964 to 1971, trappers provided mandibles from which teeth were extracted for age classification. If many teeth were from, say, 1-year-old beavers, then such animals were probably common in the population. If the number of teeth from 2-year-old beavers was low, then we know there was high mortality for the 1-year-old age class. From the mandible data, researchers constructed a life table (**Table 9.1**). The number of individuals alive at the start of the time period, in this case a year, is referred to as  $n_x$ , where  $n$  is the number and  $x$  refers to the beginning of a particular age class. By subtracting the value of  $n_x$  from the number alive at the start of the previous year, we can calculate the number dying in a given age class or year,  $d_x$ . Thus

**Table 9.1** Life table for the beaver, *Castor canadensis*, in Newfoundland, Canada.

Age class, $x$	Number alive at start of year, $n_x$	Number dying during year, $d_x$
0–1	3,695	1,995
1–2	1,700	684
2–3	1,016	359
3–4	657	286
4–5	371	98
5–6	273	68
6–7	205	40
7–8	165	38
8–9	127	14
9–10	113	26
10–11	87	37
11–12	50	4
12–13	46	17
13–14	29	7
14 +	22	22

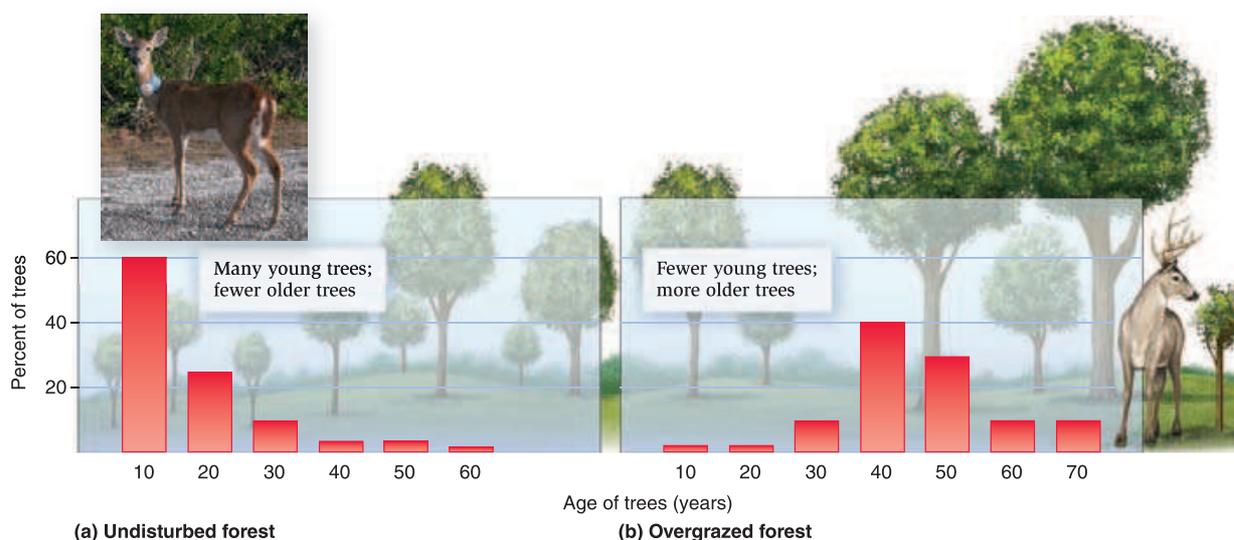
From data in Payne (1984).

$d_x = n_x - n_{x+1}$ . For example, in Table 9.1, 273 beavers were alive at the start of their sixth year ( $n_6$ ) and only 205 were alive at the start of the seventh year ( $n_7$ ); thus, 68 died during the sixth year:  $d_6 = n_6 - n_7$ , or  $d_6 = 273 - 205 = 68$ .

As mentioned at the beginning of the chapter, Adolf Murie collected detailed data on the survivorship of the Dall mountain sheep. In 1947, Edward Deevey put Murie's data in the form of a life table that listed each age class and the

number of skulls in it (**Table 9.2**). While Murie had collected 608 skulls, Deevey expressed the data per 1,000 individuals to allow for comparison with other life tables.

Deevey calculated several other valuable statistics from Murie's data. First, he was interested in survivorship. Second, he wanted to know the mortality rate within each age class. Third, he calculated the life expectancy of sheep at various ages.



**Figure 9.1** Theoretical age distribution of two forest tree populations. (a) Age distribution of an undisturbed forest with numerous young trees, many of which die as the trees age and compete with one another for resources, leaving relatively few big, older trees. (b) Age distribution of a forest where overgrazing has reduced the abundance of young trees, leaving mainly trees in the older age classes.

**Table 9.2** Static life table for the Dall mountain sheep, *Ovis dalli*, based on the known age at death of 608 sheep dying before 1937.\*

Age class	Number alive	Number dying	Proportion surviving	Mortality rate	Average no. alive in age class	Total years lived	Life Expectancy
$x$	$n_x$	$d_x = (n_x - n_{x+1})$	$l_x (= n_x/n_0)$	$q_x (= d_x/n_x)$	$L_x (= n_x + n_{x+1})/2$	$T_x = \sum L_x$	$e_x (= T_x/n_x)$
0-1	1000	199	1.000	.199	900.5	7053	7.0
1-2	801	12	0.801	.015	795	6152.5	7.7
2-3	789	13	0.789	.016	776.5	5357.5	6.8
3-4	776	12	0.776	.015	770	4581	5.9
4-5	764	30	0.764	.039	749	3811	5.0
5-6	734	46	0.734	.063	711	3062	4.2
6-7	688	48	0.688	.070	664	2351	3.4
7-8	640	69	0.640	.108	605.5	1687	2.6
8-9	571	132	0.571	.231	505	1081.5	1.9
9-10	439	187	0.439	.426	345.5	576.5	1.3
10-11	252	156	0.252	.619	174	231	0.9
11-12	96	90	0.096	.937	51	57	0.6
12-13	6	3	0.006	.500	4.5	6	1.0
13-14	3	3	0.003	1.00	1.5	1.5	0.5

\*Data are expressed per 1,000 individuals.

Survivorship, or  $l_x$ , is calculated by dividing the number of individuals in an age class by the number in the original cohort; that is,

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

(number surviving this year)  
(total number born)

Survivorship to the sixth age class (5–6 years) is therefore 734/1,000, or 0.734. This value tells us that over three-quarters of those individuals born will survive to at least 5 years old.

The mortality rate within each age class is estimated by the variable  $q_x$ , which is calculated as

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

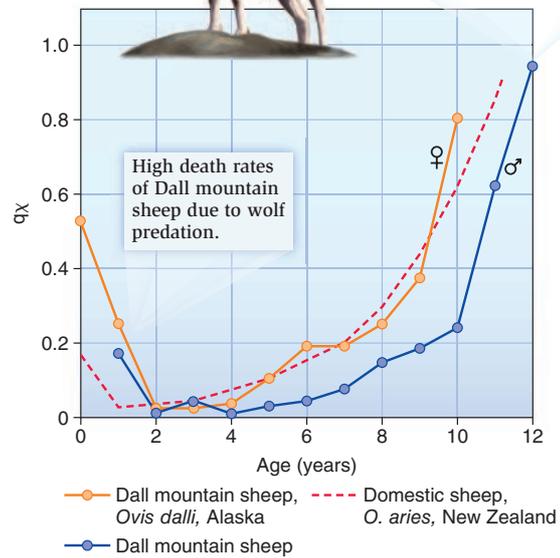
(age-specific mortality)  
(number dying)  
(number surviving)

This equation expresses the number of deaths during an age class ( $d_x$ ) as a proportion of the number of individuals that were alive at the beginning of that age class ( $n_x$ ). It gives a valuable measure of proportional mortality within an age class. For example, in the sixth age class (5–6 years), there were 46 deaths out of 734 individuals, so  $q_x = 46/734$ , or 0.063. This mortality rate allows us to determine whether mortality increases with age, decreases with age, or is independent of age. In the Dall mountain sheep,  $q_x$  is high in the first age class, meaning a lot of young sheep die. Then  $q_x$  drops dramatically and remains low until about age 8, when it increases quickly. Murie suggested that the high mortality of both young and old sheep may have been due to wolves. He thought straying youngsters were easily picked off and older animals became arthritic and were easily chased down. Such predation would not be expected to dramatically reduce the sheep population because it was not affecting reproductive females. The Park Service eventually ended a limited wolf control program that had been in effect since 1929. However, Graham Caughley (1966) compared the mortality rates of Dall mountain sheep with domestic sheep in New Zealand where wolf predation is absent (Figure 9.2). It is interesting that the mortality rates between these two species are very similar in all ages except in lambs. This suggests that Murie was correct about wolf predation impacting young sheep, but it also suggests that if old Dall sheep were not preyed on by wolves, they would have died in some other way. The data also show that mortality rates for female Dall mountain sheep are greater than for males.

Another parameter that Deevey estimated was life expectancy, the average number of additional age classes an individual can expect to live at each age. This calculation requires two intermediate steps. First, the average number of individuals alive in each age class,  $L_x$ , must be calculated.



High death rates of Dall mountain sheep in Alaska and domestic sheep in New Zealand as both populations age.



**Figure 9.2** Comparison of age-specific mortality,  $q_x$ , between Dall mountain sheep, *Ovis dalli*, in Alaska and domestic sheep, *Ovis aries*, in New Zealand. Note that the data for males and females are provided for Dall mountain sheep for all years except those in their first year. The similarities between the curves later in life suggest wolf predation does not greatly affect older Dall sheep. (After Caughley, 1966.)

Individuals may die at the beginning of an age class or at the end. Since  $n_x$  is the average number of individuals alive at the beginning of each age class, and  $n_{x+1}$  is the number alive at the beginning of the next age class, the number alive during an age class can be estimated by the relationship:

$$L_x = \frac{n_x + n_{x+1}}{2}$$

A numerical example, from the sixth and seventh rows of the data is

$$L_5 = \frac{n_5 + n_6}{2} = \frac{734 + 688}{2} = 711$$

On average, at any point in time, one could expect to find 711 individuals alive in the sixth age class. Of course, they could all die right at the beginning of the age class, or right at the end, but chances are good that about 711 would be alive at the midpoint in time of the age class. The second step in determining life expectancy is to calculate a quantity called total years lived,  $T_x$ . This is a purely intermediate step and, unlike the other columns in a life table, is without real

biological meaning.  $T_x$  is calculated by summing the values of  $L_x$  in age class  $x$  and all subsequent (older) age classes. Thus,

$$T_x = \sum_x^{\infty} L_x$$

The value of  $T_x$  for the 5-year-old sheep (sixth age class) is therefore:

$$\begin{aligned} T_6 &= L_6 + L_7 + L_8 + L_9 + L_{10} + L_{11} + L_{12} + L_{13} \\ &= 711 + 664 + 605.5 + 505 + 345.5 + 174 + \\ &51 + 4.5 + 1.5 = 3,062 \end{aligned}$$

The sheep's life expectancy, can now be calculated as follows:

$$e_x = \frac{T_x}{n_x}$$

The value of  $e_x$  indicates the average number of additional age classes an individual can expect to live at each age, so

$$e_6 = \frac{3,062}{734} = 4.2$$

Therefore, 5-year-old sheep can be expected to live, on average, for another 4.2 years.

Taken as a whole, these calculations allow important features of a population to be quantified: What is the life expectancy of individuals in this population? How does survivorship change with age? When in an individual's life is the mortality rate highest? The life expectancy of sheep actually increases in the second age class, indicating that newborn sheep struggle to survive.

Despite the value of static life tables, there are some assumptions that limit their accuracy. Paramount among these is the assumption that equal numbers of offspring are born each year. For example, if the rate of mortality of 2-year-old sheep were identical to the rate of 4-year-old sheep but there were more 2-year-old sheep born because of favorable climate in that particular year, then more skulls of 2-year-old sheep would be found later on and a higher rate of mortality of 2-year-olds would be assumed. There is often no independent method for estimating the birth rates of each age class. In addition, there are methodology difficulties in constructing static life tables. It is often difficult to accurately assess the age structure of population. In some cases, growth rings on trees, on fish scales, or on horns of ungulates make it possible to determine the age of an animal. Annual growth rings also occur in the genital plates of sea urchins and the shells of some mollusks, but this is relatively unusual. Perhaps for these reasons, the cohort life table is often reported.

### 9.1.3 Cohort life tables follow an entire cohort of individuals from birth to death

In cases where cohort life tables are constructed, population censuses must be conducted frequently but only for a limited time, usually less than a year for insects or annual plants. In

**Table 9.3** Life table for the American robin, *Turdus migratorius*.

Age (years)	$n_x$	$d_x$	$l_x$	$\log n_x$
0-1	568	286	1.00	3
1-2	282	152	0.497	2.70
2-3	130	79	0.239	2.36
3-4	51	34	0.099	1.99
4-5	17	11	0.036	1.56
5-6	6	4	0.010	1
6-7	2	0	0.006	0.78

From data in Farner (1945). Based on returns of 568 birds banded as nestlings.

these cases, the age classes may be weeks or months not years. For other organisms, like many birds or small mammals, an annual or biannual census for up to 10 years will suffice (see **Feature Investigation**). A cohort life table for the American robin, *Turdus migratorius*, based on banded nestlings that were subsequently recensused, is shown in **Table 9.3**.

### 9.1.4 Survivorship curves present survival data graphically

Organismal survival, from both static or cohort life tables, can be quickly compared by representing the data graphically, creating what is known as a survivorship curve. For example, using the data from the beaver life table, we can plot the numbers of surviving individuals against age (**Figure 9.4**). The value of  $n_x$ , the number of individuals, is typically expressed on a log scale. Ecologists use a log scale to examine rates of change with time, not change in absolute numbers. Also, the use of logs makes it easier to examine a wide range of population sizes. For example, if we start with 1,000 individuals and 500 are lost in year 1, the log of the decrease is

$$\log_{10}1,000 - \log_{10}500 = 3.0 - 2.7 = 0.3 \text{ per year.}$$

This does not mean a rate of loss of 0.3 beavers per year, rather it is the difference between the starting and ending population sizes, where both are expressed on a log scale. If we start with 100 individuals and 50 are lost, the log of the decrease is similarly

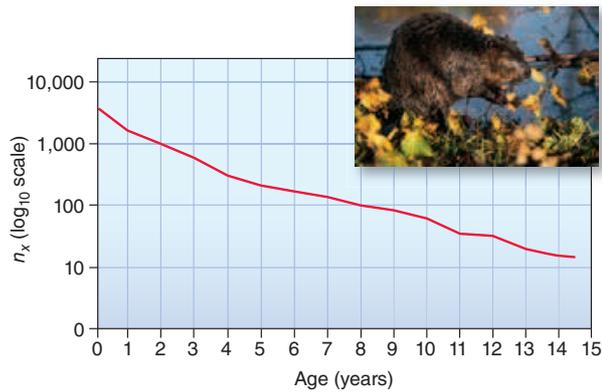
$$\log_{10}100 - \log_{10}50 = 2.0 - 1.7 = 0.3 \text{ per year.}$$

In both cases the rates of change, 0.3 per year, are identical even though the absolute numbers are different. Plotting the  $n_x$  data on a log scale ensures that regardless of the size of the starting population, the rate of change of one survivorship curve can more easily be compared to that of another species. On a log scale, the survivorship curve for the beaver is almost a diagonal line, meaning that it follows a fairly uniform rate of death over its life span.

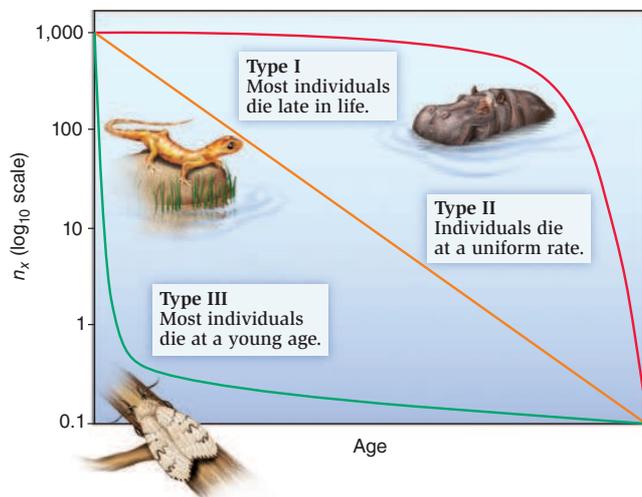
## Feature Investigation

### Frederick Barkalow, Jr., and Colleagues Constructed a Cohort Life Table for the Eastern Gray Squirrel

The Eastern gray squirrel, *Sciurus carolinensis*, is one of the most important game animals in North America. Wildlife biologists were interested to evaluate the effects of artificial nest boxes on populations. Their hope was that nest boxes would increase squirrel survival and population densities. As a first step in understanding squirrel survival they constructed a cohort life table in an area without nest boxes. In this case, the researchers based their conclusions on the survival of 493 male squirrels and 530 females marked at between 1 and 7 weeks of age. The survival of every marked squirrel was followed for all years after being marked. In this case, however, the marking occurred not all in one year, but was spread out over 8 years, between 1956 and 1963. The team did not have the resources to band all the squirrels at one time. The data from all years was compiled into a composite life table. Barkalow and colleagues marked a total of 1,023 squirrels but, as Deevey had done with the Dall mountain sheep, they converted their data to survival of a cohort of 1,000 squirrels for ease of comparison with other organisms (Figure 9.3). Life expectancy of newborn squirrels was short, about one year, but improved to over two years once squirrels had survived their first year. This is because the mortality for baby squirrels is concentrated early in their first year and a different formula was used to calculate average number alive in year 1, which is 538.9, (lower than 623.6, calculated using the standard method, i.e.,  $(1,000 + 247.3)/2 = 623.6$ ). Although the data is not shown here, nest boxes did increase squirrel survival by reducing mortality associated with predation and bad weather that was experienced in natural cavities for both young and adult squirrels.



**Figure 9.4** Survivorship curve for the North American beaver. The survivorship curve is generated by plotting the number of surviving beavers,  $n_x$ , from any given cohort of young, usually measured on a log scale, against age.



**Figure 9.5** Idealized survivorship curves.

#### ECOLOGICAL INQUIRY

Which type of survivorship curves would be typical of a butterfly, a turtle, and a human, respectively?

Survivorship curves generally fall into one of three patterns (Figure 9.5). In a type I curve, the rate of loss for juveniles is relatively low, and most individuals are lost later in life, as they become older and more prone to sickness and predators. Organisms that exhibit type I survivorship have relatively few offspring but invest much time and resources in raising their young. Many large mammals, including humans, exhibit type I curves. Survivorship for the Dall mountain sheep in Denali National Park best fits a type I curve (Figure 9.6). There is a slight initial decline in survivorship as young lambs are lost and then the survivorship curve flattens out, indicating that the sheep survive well through

**HYPOTHESIS** Nest boxes impact the survivorship of American squirrels.

**STARTING LOCATION** North Carolina, U.S.A.

**Conceptual level**

**Experimental level**

1 Mark and recapture squirrels at yearly intervals.



Establish nest boxes and mark and sex nestlings at yearly intervals. Nestlings were toe-clipped and given ear tags when recaptured.

2 Record recaptures of tagged squirrel every year. Animals failing to be recaptured are counted as dead.

Table (a)

3 Establish a composite life table for the squirrel. This table uses data from all years to create one survivorship table. The known number of survivors for year 1 is the summed number of survivors for year 1 following each tagging event. For any year this is the diagonal sum of all the columns. For example, the survivors for year 1 is 8 for 1957, 60 for 1958, 61 for 1959, 58 for 1960, 19 for 1961, 4 for 1962, 18 for 1963, and 25 for 1964, giving a total of 253.

Table (b)

4 Calculate mortality rates and life expectancy.

Table (c)

5 **THE DATA**

(a)

Year Marked	Nestlings Marked	1957	1958	1959	1960	1961	1962	1963	1964
1956	40	8	4	3	2	0	0	0	0
1957	138		60	30	28	13	9	4	3
1958	229			61	26	12	10	7	3
1959	193				58	26	19	12	9
1960	162					19	13	8	6
1961	99						4	1	1
1962	82							18	6
1963	80								25



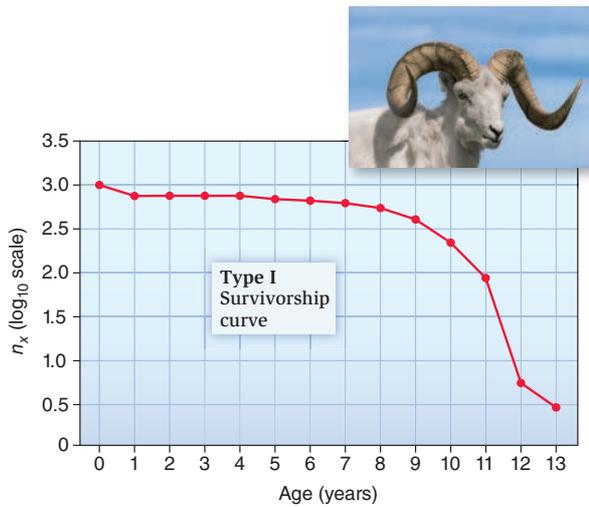
(b)

Age, x	Total Known Alive	Maximum Available for Recapture	Known Alive Per 1,000 Available
0-1	1,023	1,023	1,000.00
1-2	253	1,023	247.3
2-3	106	943	112.4
3-4	71	861	82.5
4-5	43	762	56.4
5-6	25	600	41.7
6-7	7	407	17.2
7-8	3	178	16.9

(c)

Age, x	$n_x$	$d_x$	$q_x$	$L_x$	$T_x$	$e_x$
0-1	1,000.0	752.7	0.753	538.9	989.6	0.99
1-2	247.3	134.9	0.545	179.9	450.7	1.82
2-3	112.4	29.9	0.266	97.4	270.8	2.41
3-4	82.5	26.1	0.316	69.5	173.4	2.10
4-5	56.4	14.7	0.261	49.0	103.9	1.84
5-6	41.7	24.5	0.588	29.4	54.9	1.32
6-7	17.2	0.3	0.017	17.1	25.5	1.48
7-8	16.9	16.9	1.000	8.4	8.4	0.50

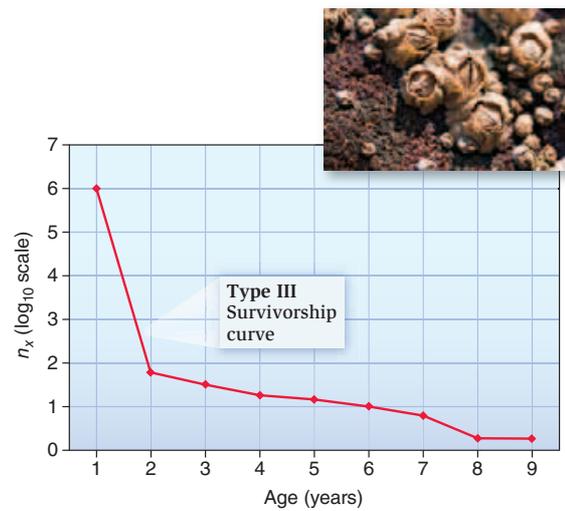
**Figure 9.3** Life table for the American Squirrel, *Sciurus carolinensis*, in North Carolina. (After Barkalow, et al., 1970.)



**Figure 9.6** Survivorship curve for the Dall mountain sheep, *Ovis dalli*.

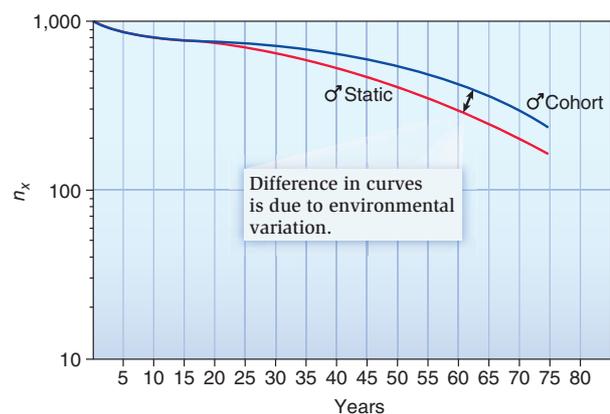
about age 7 or 8. Then the number of sheep decline rapidly as they age. These data underlined what Murie had previously observed, which was that death rates are greatest for the youngest and oldest members of the population. At the other end of the scale is a type III curve, in which the rate of loss for juveniles is relatively high, and the survivorship curve flattens out for those organisms that have avoided early death. Many fish and marine invertebrates fit this pattern. Most of the juveniles die or are eaten, but a few reach a favorable habitat and thrive. For example, many juvenile barnacles are lost at sea but, once they find a suitable rock face on which to attach themselves, barnacles grow and survive very well. A survivorship curve for the barnacle *Balanus glandula* at Washington State shows huge mortality in the first year of life (Figure 9.7). Many insects and plants also fit the type III survivorship curve, because they lay many eggs or release hundreds of seeds, respectively, and most of these die. Type II curves represent a middle ground, with fairly uniform death rates over time. Species with type II survivorship curves include many birds, small mammals, reptiles, and some annual plants. The beaver population we talked about earlier most closely resembles this survivorship curve. Keep in mind, however, that these are generalized curves and that few populations fit them exactly. Furthermore, humans can impact the survival of various species that they harvest, depending on what age classes are impacted (see **Global Insight**).

What's the difference in accuracy between a static and a cohort life table? It is very difficult to get data for both types of life table for most populations to compare the two techniques, but for humans it is possible because we can use birth and death records for people of all ages censused at a certain time and we can follow a cohort of individuals born at this same time. For example, let's examine the survivor-



**Figure 9.7** Survivorship curve for the barnacle, *Balanus glandula*.

ship of some of the British peerage born in 1800 in England, for which there is good data, and follow them for their entire lives to obtain a cohort survivorship curve. We can also take a cross section of a hypothetical English population at 1812 to get a static survivorship curve (Figure 9.10). The 1812 static curve actually relates to people born before 1812, while the cohort table gives us information on death rates after 1800. In an 1812 static survivorship curve, 72-year-old people would have been born in 1750 and fewer would have survived to 1812, compared to 70-year-old people born in 1812 and still living in 1882, because medicine and diet had improved. Thus, static curves ignore environmental variation because their predictions of how many 70-year-olds will be alive in 1882 is based on data collected from 70-year-olds in 1812, and it ignores medical and dietary improvements.



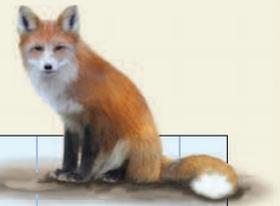
**Figure 9.10** Comparison of a cohort survivorship curve for humans born in 1800 with a static survivorship curve for 1812. (After Hutchinson, 1978.)



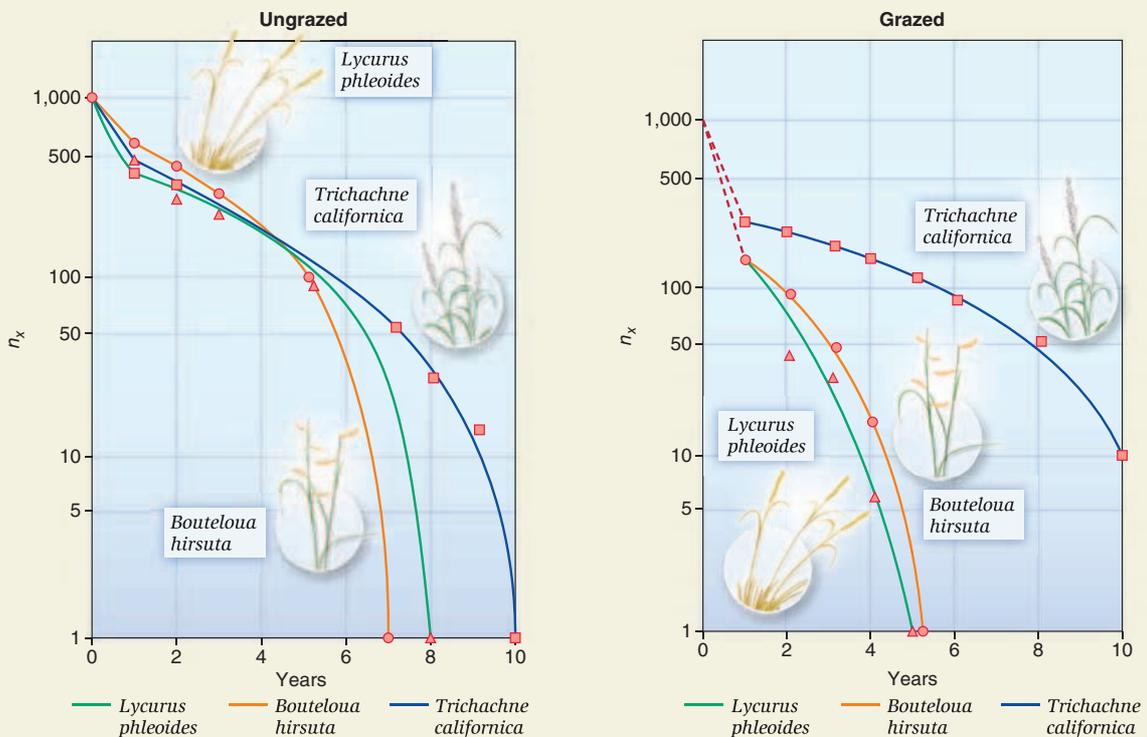
## Hunting, Overcollecting, and Grazing Can Greatly Affect Survivorship Curves

Hunting can change the appearance of an animal's survivorship curve, just as grazing pressure from herbivores can change survivorship curves for plants. The removal of trophy males (deer with large antlers or antelopes with large horns) can impact mortality rates as can the removal of large fish, especially as many large fish are females. In southern Arizona, grazing by cattle reduces the life expectancy of the grasses hairy grama, *Bouteloua hirsuta*, and common wolfstail, *Lycurus phleoides* (Figure 9.8). However, grazing appears to increase the life expectancy of cottontop, *Trichachne californica*. Presumably the preferred and competitively dominant grasses are eaten first, leaving the less preferred species to thrive in the absence of competition.

The effect of humans can be seen in an examination of survivorship curves of species considered to be pests in some urban areas. Figure 9.9 shows survivorship curves for populations of foxes, *Vulpes vulpes*, in two cities in England: London in the southeast and the smaller city of Bristol in the southwest. Fox control is practiced in London via trapping, gassing, and digging out litters of cubs, but not in Bristol. Mortality of cubs is higher in London than in Bristol, as it is for mortality in most other age classes. As a result, the fox population was 20% lower in an area of London that was the same size as Bristol.



**Figure 9.9** Survivorship curves for foxes, *Vulpes vulpes*, in London, where control is practiced, and Bristol, where no control occurs. (From data in Harris and Smith, 1987.)



**Figure 9.8** Survivorship curves for grazed and ungrazed grasses in Arizona. (After Sarukhan and Harper, 1973.)

In the natural world, environmental variation includes years of good and bad climate or food supply. This means that in reality, the cohort life table is always more accurate than the static life table. Unfortunately, we do not always have the time and resources to follow populations of organisms from birth to death, particularly if they are long-lived. Static life tables are therefore a quicker and cheaper method to get a rough idea of how the individuals of a population are distributed among age classes.

### Check Your Understanding

**9.1** The following data refer to the survivorship of red deer on a Scottish island. Complete the table by calculating the  $q_x$  column.

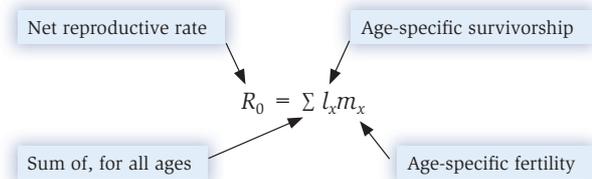
Age (years) $x$	Proportion of original cohort surviving to the beginning of age-class $x$ $l_x$	Mortality rate $q_x$
1	1.000	
2	1.000	
3	0.939	
4	0.754	
5	0.505	
6	0.305	
7	0.186	
8	0.132	
9	0.025	

## 9.2 Age-Specific Fertility Data Can Tell Us When to Expect Population Growth to Occur

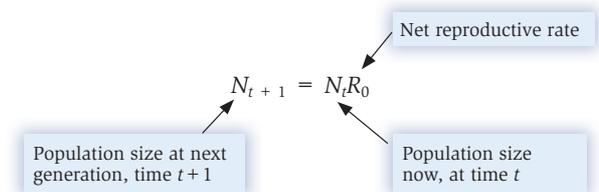
To calculate how a population grows, we need information on birth rates as well as mortality and survivorship rates. For any given age, we can determine the proportion of female offspring that are born to females of reproductive age. Using these data we can determine an **age-specific fertility** rate, called  $m_x$ . For example, if 100 females at age  $x$  produce 75 female offspring,  $m_x = 0.75$ , which means that, on average, each female of age  $x$  produces 0.75 female offspring in that year. With this additional information, we can calculate the growth rate of a population. First, we use the survivorship data to find the proportion of females alive at the start of any given age class. Recall that the survivorship rate, termed  $l_x$ , equals  $n_x/n_0$ , where  $n_0$  is the number alive at time 0, the start of the study, and  $n_x$  is the number alive at the beginning of age class  $x$ . Let's return to the beaver life table (Table 9.4). The proportion of the original beaver population still alive at the start of the sixth age class,  $l_6$ , equals  $n_6/n_0 = 273/3,695$ , or 0.074. This means that 7.4% of the original beaver population survived to age 6. Next we multiply the data in the two columns,  $l_x$  and  $m_x$ , for each row, to give us

a column  $l_x m_x$ , an average number of offspring per female. This column represents the contribution of each age class to the overall population growth rate. An examination of the beaver age-specific fertility rates illustrates a couple of general points. First, for this beaver population in particular, and for many organisms in general, there are no babies born to young females. Next, as females mature sexually, age-specific fertility goes up and remains fairly high until later in life, when females reach postreproductive age.

The number of offspring born to females of any given age class depends on two things: the number of females in that age class and their age-specific fertility rate. Thus, although fertility of young beavers is very low, there are so many females in the age class that  $l_x m_x$  for 1-year-olds is quite high. Age-specific fertility for older beavers is much higher, but the relatively few females in these age classes cause  $l_x m_x$  to be low. Maximum values of  $l_x m_x$  occur for females of an intermediate age, 3–4 years old in the case of beaver. The overall growth rate per generation is the number of offspring born to all females of all ages, where a generation is defined as the mean period between birth of females and birth of their offspring. Thus, to calculate the generational growth rate, we sum all the values of  $l_x m_x$ , that is,  $\sum l_x m_x$ , where the symbol  $\Sigma$  means "sum of." This summed value,  $R_0$ , is called the **net reproductive rate**, the average number of female offspring produced by all the females in a population over the course of a generation where a generation constitutes the reproductive life of a female.



To calculate the future size of a population, we simply multiply the number of females in the population by the net reproductive rate. Thus, the population size in the next generation,  $N_{t+1}$ , is determined by the number in the population now, at time  $t$ , which is given by  $N_t$ , multiplied by  $R_0$ .



Let's consider a theoretical example in which the number of beavers alive now,  $N_t$ , is 1,000 and  $R_0 = 1.1$ . This means the beaver population is reproducing at a rate that is 10% greater than simply replacing itself. The size of the population next generation,  $N_{t+1}$ , is given by

$$\begin{aligned}
 N_{t+1} &= N_t R_0 \\
 N_{t+1} &= 1,000 \times 1.1 \\
 &= 1,100
 \end{aligned}$$

**Table 9.4** Life table and age-specific fertility rates for the beaver, *Castor canadensis*, in Newfoundland, Canada. This information allows us to calculate the net reproductive rate per generation,  $R_0$ .

Age class, $x$	Number alive at start of year, $n_x$	Number dying during year, $d_x$	Proportion alive at start of age interval, $l_x$	Age-specific fertility, $m_x$	Average number of offspring per age class $l_x m_x$	$\times l_x m_x$
0-1	3,695	1,995	1.000	0.000	0	0
1-2	1,700	684	0.460	0.315	0.145	0.145
2-3	1,016	359	0.275	0.400	0.110	0.220
3-4	657	286	0.178	0.895	0.159	0.477
4-5	371	98	0.100	1.244	0.124	0.496
5-6	273	68	0.074	1.440	0.107	0.535
6-7	205	40	0.055	1.282	0.071	0.426
7-8	165	38	0.045	1.280	0.058	0.406
8-9	127	14	0.034	1.387	0.047	0.376
9-10	113	26	0.031	1.080	0.033	0.297
10-11	87	37	0.024	1.800	0.043	0.430
11-12	50	4	0.014	1.080	0.015	0.165
12-13	46	17	0.012	1.440	0.017	0.204
13-14	29	7	0.007	0.720	0.005	0.065
14+*	22	22	0.006	0.720	0.009	0.126
Net reproductive rate, $\sum l_x m_x = 0.938$						4.368

\*Last row gives a summary of data for all beavers ages 14 and older. From data in Payne (1984).

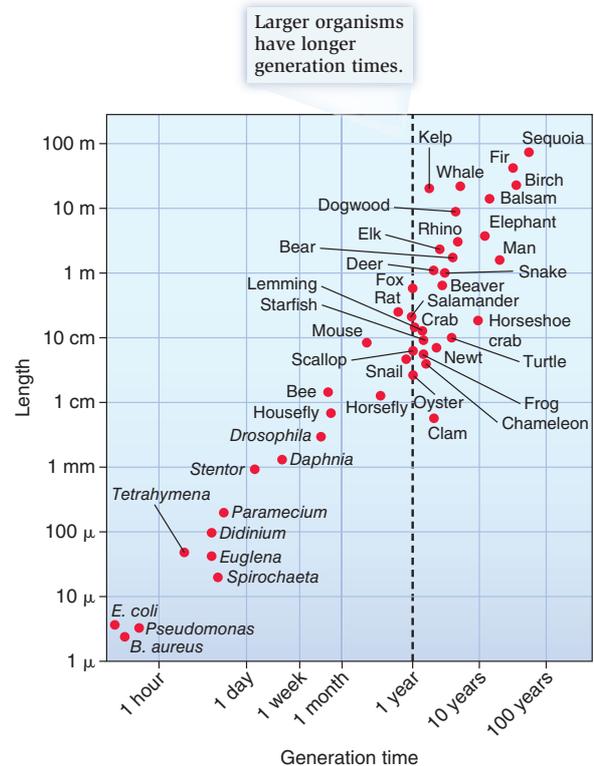
Thus, the number of beavers in the next generation is 1,100 and the population will have grown larger. How long is a beaver generation? Population ecologists generally refer to a generation time,  $T$ , as the average time for a female organism to grow from a fertilized egg and produce more fertilized eggs. We can calculate  $T$  from our life table by multiplying the  $l_x m_x$  column by  $x$ , the age in years, summing the column and dividing by  $R_0$ . Here we assume that all the babies born to mothers over their lifetimes were born to them at some age,  $T$ , instead. We are thus calculating a mean age of reproduction.

$$\text{Thus, } T = \frac{\sum x l_x m_x}{R_0}$$

$$\text{For our beaver data, } T = \frac{4.368}{0.938} = 4.657$$

The average generation time for beaver in Newfoundland is about 4.6 years. Generally, generation time increases as organismal size increases (Figure 9.11).

In determining population growth, much depends on the value of  $R_0$ . If  $R_0 > 1$ , then the population will grow. If  $R_0 < 1$ , the population is in decline. If  $R_0 = 1$ , then the population size stays the same and we say it is at **equilibrium**. In the case of the beavers, Table 9.4 reveals that  $R_0 = 0.938$ , which is less than 1, and therefore the population is in decline. This is valuable information, because it tells us that at that time, the beaver population in Newfoundland needed more protection, perhaps in the form of limits on trapping and hunting, in order to attain a population level at equilibrium.



**Figure 9.11** The relationship of length and generation time for a variety of organisms. (After Bonner, 1965.)

In his study of the barnacles of Washington State, Joe Connell (1970) also provided age-specific fertility data (Table 9.5). Connell was interested in determining which factors were most important in influencing population sizes of barnacles and to do this he gathered life table and fertility data. Despite huge mortality of young stages, barnacles 1 year old or older were very fertile, and Connell estimated each female could lay up to 12,700 eggs. With such high levels of egg production, the population had a net reproductive rate,  $R_0$ , of 1.282 and was increasing. Most of the offspring are produced by adults between 1 and 4 years old because survival of older age classes is poor. Generation time,  $T$ , was about 3.1 years. Predation by several species of snails of the genus *Thais* proved to be the most influential factor on population size though the data are not shown here.

**Table 9.5** A life table and age-specific fertility for the barnacle, *Balanus glandula*.

Age (years) $x$	Number of survivors $n_x$	$l_x$	$m_x$	$l_x m_x$	$x l_x m_x$
0	1,000,000	1.000	0	0	
1	62	0.0000620	4,600	0.285	0.285
2	34	0.0000340	8,700	0.296	0.592
3	20	0.0000200	11,600	0.232	0.696
4	15.5	0.0000155	12,700	0.197	0.788
5	11	0.0000110	12,700	0.140	0.700
6	6.5	0.0000065	12,700	0.082	0.492
7	2	0.0000020	12,700	0.025	0.175
8	2	0.0000020	12,700	0.025	0.200

From data in Connell (1970).

### Check Your Understanding

**9.2** The following data is a fertility table for the wildebeest, *Connochaetes taurinus*, in Africa. Calculate  $R_0$  and  $T$ , generation time.

$x$	$l_x$	$m_x$
0	1.00	0
1	0.80	0
2	0.70	0.11
3	0.63	0.46
4	0.57	0.46
5	0.41	0.46
6	0.31	0.46
7	0.23	0.46
8	0.17	0.46
9	0.14	0.46
10	0.14	0.46
11	0.12	0.46
12	0.09	0.46
13	0.06	0.46
14	0.05	0.46
15	0.04	0.46
16	0.02	0.46

## SUMMARY

- Populations of many species exhibit distinct age classes. The distribution of individuals within age classes may later be affected by other phenomena such as natural enemies (Figure 9.1).
- Static life tables provide a snapshot of a population's age structure and survivorship and mortality of individuals in different age classes (Tables 9.1, 9.2, Figure 9.2).
- Cohort life tables provide similar information but follow an entire cohort of individuals from birth to death (Table 9.3, Figure 9.3).
- Survivorship curves illustrate life tables by plotting the numbers of surviving individuals at different ages (Figure 9.4).
- Survivorship curves generally fall into one of three types: Type III, with high juvenile mortality, Type II with constant mortality throughout life, or Type I, with high juvenile survival (Figures 9.5–9.7).
- Hunting and overgrazing can cause large changes in survivorship curves (Figures 9.8, 9.9).
- Survivorship curves generated from static life tables may be easier to construct but they ignore environmental variation and may be slightly less accurate than survivorship curves from cohort life tables (Figure 9.10).
- Age-specific fertility and survivorship data help determine the overall growth rate per generation, or the net reproductive rate ( $R_0$ ) (Tables 9.4, 9.5).
- Generally, generation time increases as organismal size increases (Figure 9.11).



## DATA ANALYSIS

1. The age structure for a gray squirrel population in North Carolina is given below. (a) Calculate  $l_x$ , the proportion alive at the start of each age interval. (b) If  $m_0 = 0.05$ ,  $m_1 = 1.28$ , and  $m_x$  for every other age group is 2.28, calculate  $R_0$ . Is the squirrel population increasing or decreasing?

Age in Years	$n_x$
1	134
2	56
3	39
4	23
5	12
6	5
7	2

2. Black rhinoceros, *Diceros bicornis*, skulls were collected and aged, based on mandible size from Tsavo National Park in Kenya and a life table was constructed. The number of deaths in each age class has been expressed per 1,000 individuals born. Calculate  $n_x$ ,  $l_x$ , and life expectancy,  $e_x$ . Comment on possible errors that may underestimate mortality of young rhinos. Hint: Think back to Chapter 7, Nutrients, and what can happen to young skulls.

Age, $x$	$d_x$	Age, $x$	$d_x$
0	160	20	12
1	141	21	11
2	93	22	11
3	68	23	10
4	50	24	10
5	33	25	9
6	31	26	7
7	31	27	6
8	31	28	6
9	25	29	6
10	25	30	6
11	26	31	6
12	25	32	5
13	25	33	4
14	25	34	4
15	25	35	2
16	21	36	2
17	17	37	1
18	16	38	0
19	14		