

remain vegetative for many years: in some species, 100 years. The whole population of shoots then flowers simultaneously in a mass suicidal orgy. Even when shoots have become physically separated from each other, the parts still flower synchronously.

Organisms of long-lived species that are the same age, however, are not necessarily the same size – especially in modular organisms. Some individuals may be very old but have been suppressed in their growth and development by predators or by competition. Age, then, is often a particularly poor predictor of fecundity. An analysis that classifies the members of a population according to their size rather than their age (Figure 5.9) is often more useful in suggesting whether they will survive or reproduce.

size matters

5.3 Monitoring birth and death: life tables and fecundity schedules

The previous sections have outlined the different patterns of births and deaths in different species. But patterns are just a start. What are the *consequences* of these patterns in specific cases in terms of their effects on how a population might grow to pest proportions, say, or shrink to the brink of extinction? To determine these consequences, we need to monitor the patterns in a quantitative way.

There are different ways of doing so. To monitor and quantify survival, we may follow the fate of individuals from the same *cohort* within a population: that is, all individuals born within a particular period. A *cohort life table* then records the survivorship of the members of the cohort over time (Box 5.2). A different approach is necessary when we cannot follow cohorts but we know the ages of all the individuals in a population. We can then, at one time, describe the numbers of survivors of different ages in what is called a *static life table* (Box 5.2).



5.2 Quantitative aspects

The basis for cohort and static life tables

In Figure 5.10, a population is portrayed as a series of diagonal lines, each line representing the life 'track' of an individual. As time passes, each individual ages (moves from bottom left to top right along its track) and eventually dies (the dot at the end of the track). Here, individuals are classified by their age. In other cases it may be more appropriate to split the life of each individual into different developmental stages.

Time is divided into successive periods: t_0 , t_1 , etc. In the present case, three individuals were born (started

their life track) prior to the time period t_0 , four during t_0 , and three during t_1 . To construct a *cohort life table*, we direct our attention to a particular cohort (in this case, those born during t_0) and monitor what happens subsequently to the cohort. The life table is constructed by noting the number surviving to the start of each time period. Here, two of the four individuals survived to the beginning of t_1 ; only one of these was alive at the beginning of t_2 ; and none survived to the start of t_3 . The first data column of the cohort life table

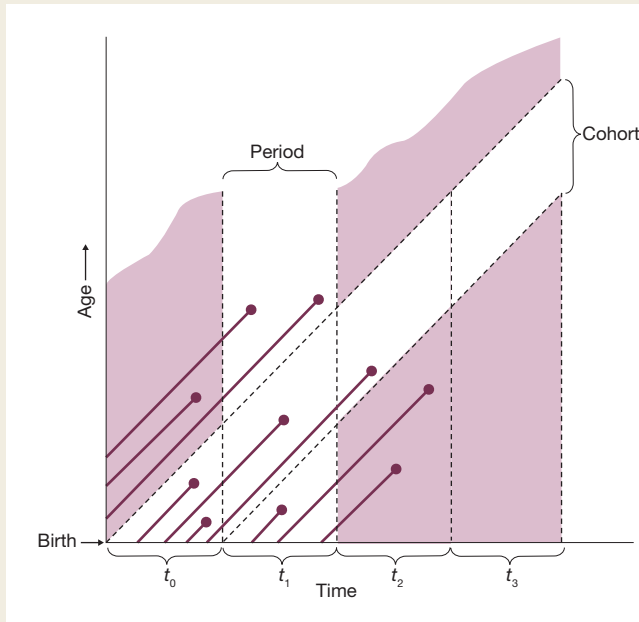


Figure 5.10

See text for details.

thus comprises the series of declining numbers in the cohort: 4, 2, 1, 0.

A different approach is necessary when we cannot follow cohorts but we know the ages of all the individuals in a population (perhaps from some clue such as the condition of the teeth in a species of deer). We can then, as the figure shows, direct our attention to the whole population during a single period (in this case, t_1) and note the numbers of survivors of different ages in the population. These may be thought of as entries in a life table *if* we assume that rates of birth and death

are, and have previously been, constant – a very big assumption. What results is called a *static life table*. Here, of the seven individuals alive during t_1 , three were actually born during t_1 and are hence in the youngest age group, two were born in the previous time interval, two in the interval before that, and none in the interval before that. The first data column of the static life table thus comprises the series 3, 2, 2, 0. This amounts to saying that over these time intervals, a typical cohort will have started with three and declined over successive time intervals to two, then two again, then zero.

The fecundity of individuals also changes with their age, and to understand properly what is going on in a population we need to know how much individuals of different ages contribute to births in the population as a whole: these can be described in *age-specific fecundity schedules*.

5.3.1 Cohort life tables

an annual life table for a plant

The most straightforward life table to construct is a cohort life table for annuals, because with non-overlapping generations it is indeed often possible to follow a single cohort from the first birth to the death of the last survivor. One such life table, for the annual plant *Phlox drummondii*, is shown in Table 5.1. An initial cohort of 996 seeds was followed from seed germination to the death of the last adult, with the life cycle broken down into successive periods of 14–63 days.

Table 5.1

A simplified cohort life table for the annual plant *Phlox drummondii*. The columns are explained in the text.

AGE INTERVAL (DAYS) $x-x'$	NUMBER SURVIVING TO DAY x a_x	PROPORTION OF ORIGINAL COHORT SURVIVING TO DAY x l_x	SEEDS PRODUCED IN EACH STAGE F_x	SEEDS PRODUCED PER SURVIVING INDIVIDUAL IN EACH STAGE m_x	SEEDS PRODUCED PER ORIGINAL INDIVIDUAL IN EACH STAGE $l_x m_x$
0–63	996	1.000	0.0	0.00	0.00
63–124	668	0.671	0.0	0.00	0.00
124–184	295	0.296	0.0	0.00	0.00
184–215	190	0.191	0.0	0.00	0.00
215–264	176	0.177	0.0	0.00	0.00
264–278	172	0.173	0.0	0.00	0.00
278–292	167	0.168	0.0	0.00	0.00
292–306	159	0.160	53.0	0.33	0.05
306–320	154	0.155	485.0	3.13	0.49
320–334	147	0.148	802.7	5.42	0.80
334–348	105	0.105	972.7	9.26	0.97
348–362	22	0.022	94.8	4.31	0.10
362–	0	0.000	0.0	0.00	0.00
Total			2408.2		2.41

AFTER LEVERICH & LEVIN, 1979

$$R_0 = \sum l_x m_x = \frac{\sum F_x}{a_0} = 2.41.$$

Even when generations overlap, if individuals can be marked early in their life so that they can be recognized subsequently, it can be possible to follow the fate of each year's cohort separately. It is then possible to merge the cohorts from the different years so as to derive a cohort life table that combines information from the whole study period. An example is shown in Table 5.2: females from a population of the yellow-bellied marmot, *Marmota flaviventris*, which was live-trapped and marked individually from 1962 through to 1993 in the East River Valley of Colorado.

The first column in each life table is a list of the age classes (or in some cases, stages) of the organism's life: 14–63-day periods for *Phlox*, years for the marmots. The second column is then the raw data from each study, collected in the field. It reports the number of individuals surviving to the beginning of each age class (see Box 5.2).

Ecologists are typically interested not just in examining populations in isolation but in comparing the dynamics of two or more perhaps rather different populations (in the presence and absence of a pollutant, for instance). Hence, it is necessary to standardize the raw data so that comparisons can be made. This is done in the third column of the table, which is said to contain l_x values, where l_x is defined as the proportion of the original cohort surviving to the start of age class. The first value in the third column, l_0 (spoken: L zero), is therefore the proportion surviving to the beginning of this original age class. Obviously, in Tables 5.1 and 5.2, and in every life table, l_0 is 1.00 (the whole cohort is there at the start).

In the marmots, for example, there were 773 females observed in this youngest age class. The l_x values for subsequent age classes are then expressed as proportions

a cohort life table for
marmots . . .

Table 5.2

A simplified cohort life table for female yellow-bellied marmots, *Marmota flaviventris*, in Colorado. The columns are explained in the text.

AGE CLASS (YEARS)	NUMBER ALIVE AT THE START OF EACH AGE CLASS	PROPORTION OF ORIGINAL COHORT SURVIVING TO THE START OF EACH AGE CLASS	NUMBER OF FEMALE YOUNG PRODUCED BY EACH AGE CLASS	NUMBER OF FEMALE YOUNG PRODUCED PER SURVIVING INDIVIDUAL IN EACH AGE CLASS	NUMBER OF FEMALE YOUNG PRODUCED PER ORIGINAL INDIVIDUAL IN EACH AGE CLASS
x	a_x	l_x	F_x	m_x	$l_x m_x$
0	773	1.000	0	0.000	0.000
1	420	0.543	0	0.000	0.000
2	208	0.269	95	0.457	0.123
3	139	0.180	102	0.734	0.132
4	106	0.137	106	1.000	0.137
5	67	0.087	75	1.122	0.098
6	44	0.057	45	1.020	0.058
7	31	0.040	34	1.093	0.044
8	22	0.029	37	1.680	0.049
9	12	0.016	16	1.336	0.021
10	7	0.009	9	1.286	0.012
11	3	0.004	0	0.000	0.000
12	2	0.003	0	0.000	0.000
13	2	0.003	0	0.000	0.000
14	2	0.003	0	0.000	0.000
15	1	0.001	0	0.000	0.000
Total			519		0.670

$$R_0 = \sum l_x m_x = \frac{\sum F_x}{a_0} = 0.67.$$

of this number. Only 420 individuals survived to reach their second year (age class 1: between 1 and 2 years of age). Thus, in Table 5.2, the second value in the third column, l_1 , is the proportion $420/773 = 0.543$ (that is, only 0.543 or 54.3% of the original cohort survived this first step). In the next row, $l_2 = 208/773 = 0.269$, and so on. For *Phlox* (Table 5.1), $l_1 = 668/996 = 0.671 = 67.1\%$ survived the first step.

In a full life table, subsequent columns would then use these same data to calculate the proportion of the original cohort that died at each stage and also the mortality rate for each stage, but for brevity these columns have been omitted here.

... and fecundity schedule ...

Tables 5.1 and 5.2 also include fecundity schedules for *Phlox* and for the marmots (columns 4 and 5). Column 4 in each case shows F_x , the total number of the youngest age class produced by each subsequent age class: this youngest class being seeds for *Phlox* and, for the marmots, independent juveniles fending for themselves outside of their burrows. Thus, *Phlox* plants produced seed between around day 300 and day 350 in the year; while marmots produced young when they were between 2 and 10 years old.

The fifth column is then said to contain m_x values, fecundity: the mean number of the youngest age class produced per surviving individual of each subsequent class. For *Phlox*, it is apparent that fecundity, m_x , the mean number of

seeds produced per surviving adult plant, reached a peak around day 340. For the marmots, fecundity was highest for 8-year-old females.

In the final column of a life table, the l_x and m_x columns are brought together to express the overall extent to which a population increases or decreases over time – reflecting the dependence of this on both the survival of individuals (the l_x column) and the reproduction of those survivors (the m_x column). That is, an age class contributes most to the next generation when a large proportion of individuals have survived and they are highly fecund, and it contributes least when few survive and/or they produce few (or no) offspring. The sum of all the $l_x m_x$ values, $\sum l_x m_x$, where the symbol Σ means ‘the sum of’, is therefore a measure of the overall extent by which this population has increased or decreased in a generation. We call this the *basic reproductive rate* and denote it by R .

For *Phlox* (Table 5.1), $R = 2.41$: this population set approximately 2.5 times more seed at the end of the generation (the end of the season) than was present at the beginning. For the marmots, $R = 0.67$: the population was declining to around two-thirds its former size each generation. However, whereas for *Phlox* the length of a generation is obvious, since, being an annual, there is one generation each year, for the marmots the generation length must itself be calculated. The details of that calculation are beyond our scope here, but its value, 4.5 years, matches what we can observe ourselves in the life table: that a ‘typical’ period from an individual’s birth to giving birth itself (i.e. a generation) is around 4.5 years. Thus, Table 5.2 indicates that each generation, every 4.5 years, this particular marmot population was declining to around two-thirds its former size.

It is also possible to study the detailed pattern of decline in either the *Phlox* cohort or a cohort of marmots. Figure 5.11a, for example, shows the numbers surviving relative to the original population – the l_x values – plotted against the age of the cohort. However, this can be misleading. If the original population is 1000 individuals, and it decreases by half to 500 in one time interval, then this decrease looks more dramatic on a graph like Figure 5.11a than a decrease from 50 to 25 individuals later in the season. Yet the risk of death to individuals is the same on both occasions. If, however, l_x values are replaced by $\log(l_x)$ values, that is, the logarithms of the values, as in Figure 5.11b (or, effectively the same thing, if l_x values are plotted on a log scale), then it is a characteristic of logs that the reduction of a population to half its original size will always look the same. *Survivorship curves* are, therefore, conventionally plots of $\log(l_x)$ values against cohort age.

Figure 5.11b shows that there was a relatively rapid and constant decline in the size of the *Phlox* cohort over the first 6 months, but that the death rate thereafter remained steady and rather low until the very end of the season, when the survivors all died. For the marmots, Figure 5.11b shows an even more clearly constant decline until around the 10th year of life (when breeding ceased), followed by a brief period with effectively no mortality, after which the few remaining survivors died.

It is possible to see, therefore, even from these two examples, how life tables can be useful in characterizing the ‘health’ of a population – the extent to which it is growing or declining – and in identifying which stage in the life cycle (whether it is survival or birth) is apparently most instrumental in determining that rate of increase or decline. Either or both of these may be vital in determining how best to conserve an endangered species or control a pest.

... combined to give the basic reproductive rate

logarithmic survivorship curves

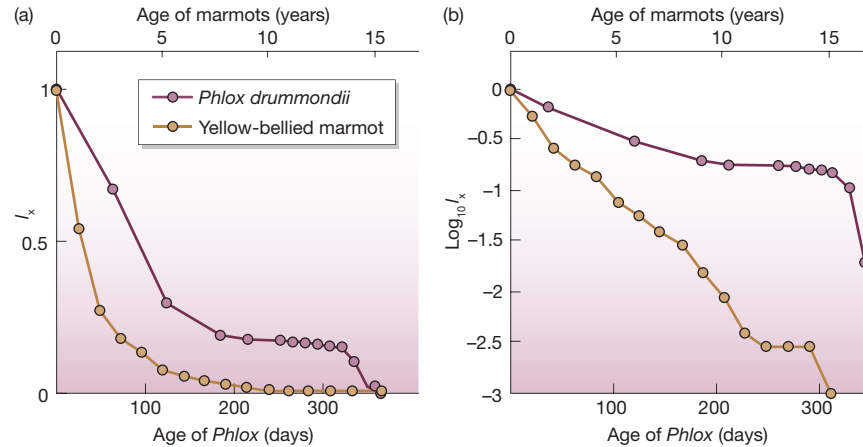


Figure 5.11

Following the survival of a cohort of *Phlox drummondii* (maroon, Table 5.1) and of the yellow-bellied marmot (yellow, Table 5.2). (a) When l_x is plotted against cohort age, it is clear that most individuals are lost relatively early in the lives of the cohorts, but there is no clear impression of the risk of mortality at different ages. (b) By contrast, a survivorship curve plotting $\log(l_x)$ against age shows, for *Phlox*, that an initial 6 months of moderate survivorship was followed by an extended period of higher survivorship (less risk of mortality) and then by very low survivorship in the final weeks of the annual cycle. For the marmots, there was virtually constant mortality risk until around age 10, followed by a brief period of low risk after which the remaining survivors died.

5.3.2 Life tables for populations with overlapping generations

Many of the species for which we have important questions, and for which life tables may provide an answer, have repeated breeding seasons like the marmots, or continuous breeding as in the case of humans, but constructing life tables here is complicated, largely because these populations have individuals of many different ages living together. Building a cohort life table is sometimes possible, as we have seen, but this is relatively uncommon. Apart from the mixing of cohorts in the population, it can be difficult simply because of the longevity of many species.

a static life table – useful if used with caution

Another approach is to construct a ‘population snapshot’ in a static life table (see Box 5.2). Superficially, the data look like a cohort life table: a series of different numbers of individuals in different age classes. But great care is required: they can only be treated and interpreted in the same way if patterns of birth and survival in the population have remained much the same since the birth of the oldest individuals – and this will happen only rarely. Nonetheless, useful insights can sometimes be gained by combining the data from a static life table (an *age structure*: the numbers in different age classes) with corresponding background information. This is illustrated by a study of two populations of the long-lived tree *Acacia burkittii* in South Australia (Figure 5.12). Although differences in age structure between the populations are obvious, the reasons are not. Fortunately, background information provides important clues.

AFTER CRISP & LANGE, 1976

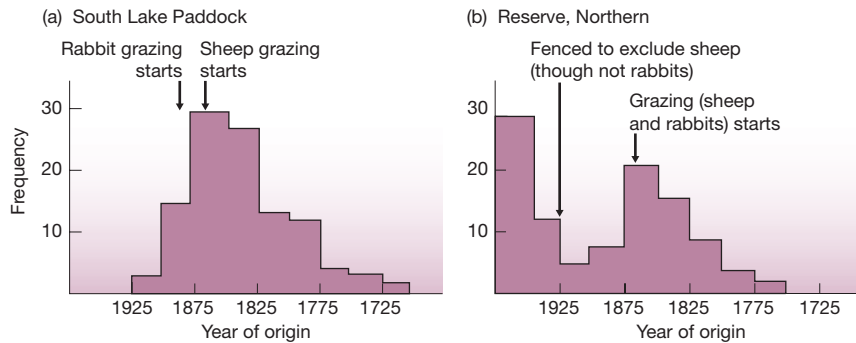


Figure 5.12

Age structures (and hence static life tables) of *Acacia burkittii* populations at two sites in South Australia. South Lake Paddock populations had been grazed by sheep from 1865 to 1970 and by rabbits from 1885 to 1970, whereas the Reserve population had been fenced in 1925 to exclude sheep (but did not exclude rabbits). With this information in hand, the effect of grazing from 1865 onward is evident in the decreased numbers of new recruits to both populations. However, the effects of fencing after 1925 are equally obvious in the Reserve population, where the proportion of new recruits increased dramatically. The effects of rabbit grazing on recruitment after fencing in the Reserve population can, however, still be detected, since, for example, the 1925–1940 age class was much smaller than the (pre-grazing) 1845–1860 class, even though the latter had survived an additional 75 years.

5.3.3 A classification of survivorship curves

Life tables provide a great deal of data on specific organisms. But ecologists search for generalities: patterns of life and death that we can see repeated in the lives of many species. Ecologists conventionally divide survivorship curves into three types, in a scheme that goes back to 1928, generalizing what we know about the way in which the risks of death are distributed through the lives of different organisms (Figure 5.13).

- In a type I survivorship curve, mortality is concentrated toward the end of the maximum lifespan. It is perhaps most typical of humans in developed countries and their carefully tended zoo animals and pets.

AFTER PEARL, 1928; DEEVEY, 1947

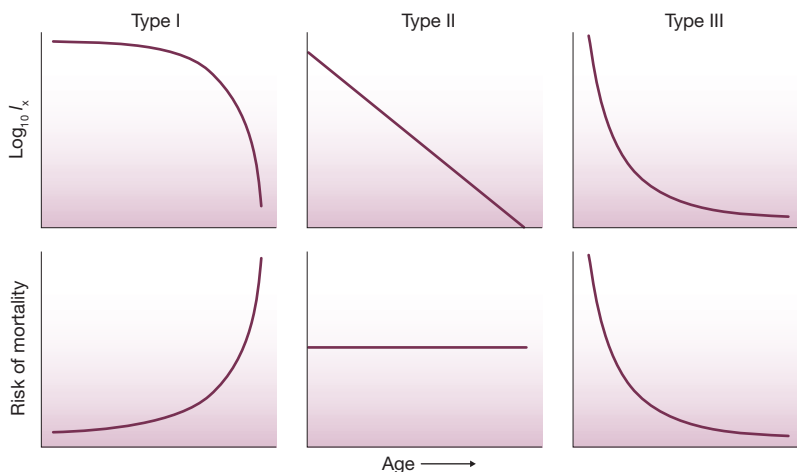


Figure 5.13

A classification of survivorship curves plotting $\log(l_x)$ against age, above, with corresponding plots of the changing risk of mortality with age, below. The three types are discussed in the text.