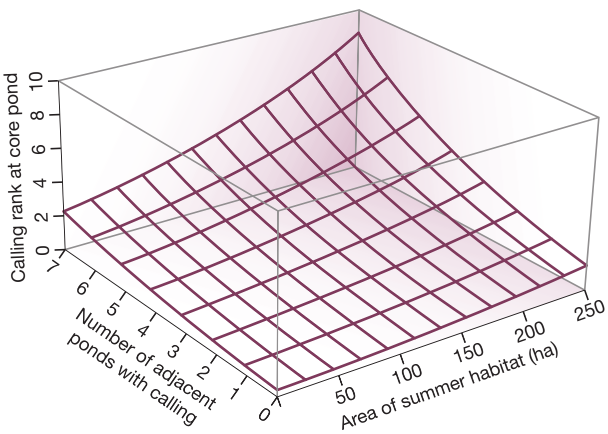


AFTER POPE ET AL., 2000

Figure 5.3

The abundance (calling rank) of leopard frogs (*Rana pipiens*) in ponds increases significantly with both the number of adjacent ponds that are occupied and the area of summer habitat within 1 km of the pond. Calling rank is the sum of an index measured on four occasions, namely: 0, no individuals calling; 1, individuals can be counted, calls not overlapping; 2, calls of <15 individuals can be distinguished with some overlapping; 3, calls of ≥15 individuals.

information on the relative size of a population, but usually give little indication of absolute size. As an example, Figure 5.3 shows how the abundance of Canadian leopard frogs was affected by the number of occupied ponds and the amount of summer (terrestrial) habitat in their vicinity. Here, frog abundance was estimated from the 'calling rank': whether there were no frogs, 'few', 'many' or 'very many' frogs calling on each of four occasions. Despite their shortcomings, even indices of abundance can provide valuable information.

Moreover, as we have already noted, for modular organisms it is often not even clear what it is we should be counting.

5.2 Life cycles

5.2.1 Life cycles and reproduction

If we wish to understand the forces determining the abundance of a population of organisms, we need to know the important phases of those organisms' lives: that is, the phases when these forces act most significantly. For this, we need to understand the sequences of events that occur in those organisms' life cycles.

There is a point in the life of any individual when, if it survives that long, it will start to reproduce and leave progeny. A highly simplified, generalized life history (Figure 5.4) comprises birth, followed by a pre-reproductive period, a period of reproduction, a post-reproductive period and then death as a result of senescence (though of course other forms of mortality may intervene at any time). The life histories of all unitary organisms can be seen as variations around this simple pattern, though a post-reproductive period (as seen in humans) is probably rather unusual.

the conflict between growth and reproduction

Some organisms fit several or many generations within a single year, some have just one generation each year (annuals) and others (perennials) have a life cycle extended over several or many years. For all organisms, though, a period of growth occurs before there is any reproduction, and growth usually slows down (and in some cases stops altogether) when reproduction starts. Growth and reproduction both require resources and there is clearly some conflict between them. Thus, as the perennial plant *Sparaxis grandiflora* enters its reproductive

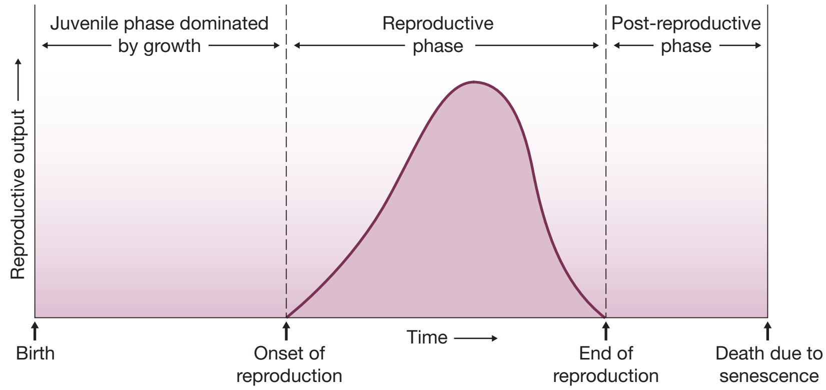


Figure 5.4

An outline life history for a unitary organism. Time passes along the horizontal axis, which is divided into different phases. Reproductive output is plotted on the vertical axis.

stage in the Southwestern Cape, South Africa, flowers, flower stalks and fruit (aspects of reproduction) can be seen to have been produced *at the expense* of roots and leaves (Figure 5.5). There are also many plants (e.g. foxgloves) that spend their first year in vegetative growth, and then flower and die in the second or a later year (called 'biennial' plants). But if the flowers of these species are removed before their seeds begin to set, the plants usually survive to the following year, when they flower again and set seed even more vigorously. It seems to be the cost of provisioning the offspring (seeds) rather than the flowering itself that is lethal. Similarly, pregnant women are advised to increase their caloric intake by as much as half their normal consumption: when nutrition is inadequate, pregnancy can harm the health of the mother.

iteroparous and semelparous species

Among both annuals and perennials, there are some – *iteroparous species* – that breed repeatedly, devoting some of their resources during a breeding episode not to breeding itself, but to survival to further breeding episodes (if they manage to live that long). We ourselves are examples. There are others, *semelparous species*, like the biennial plants already described, in which there is a single reproductive episode, with no resources set aside for future survival, so that reproduction is inevitably followed quickly by death.

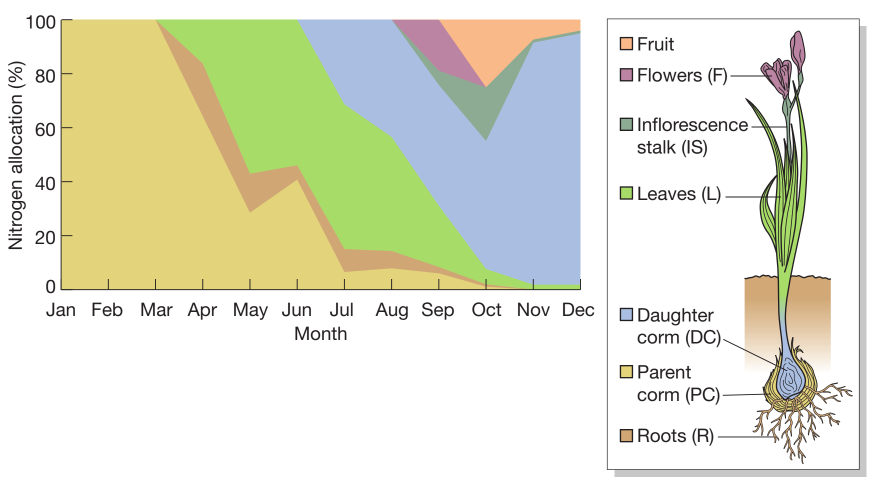


Figure 5.5

Percentage allocation of the crucial resource nitrogen to different structures throughout the annual cycle of the perennial plant *Sparaxis grandiflora* in South Africa, where it sets fruit in the southern hemisphere spring (September–December). The plant grows each year from a corm, which it replaces over the growing season, but note the development of reproductive parts at the expense of roots and leaves toward the end of the growing season. The plant parts themselves are illustrated to the right for a plant in early spring.

AFTER RUITERS & MCKENZIE, 1994

5.2.2 Annual life cycles

In strongly seasonal, temperate latitudes, most annuals germinate or hatch as temperatures start to rise in the spring, grow rapidly, reproduce and then die before the end of summer. The European common field grasshopper *Chorthippus brunneus* is an example of an annual species that is iteroparous. It emerges from its egg in late spring and passes through four juvenile stages of nymph before becoming adult in midsummer and dying by mid-November. During their adult life, the females reproduce repeatedly, each time laying egg pods containing about 11 eggs, and recovering and actively maintaining their bodies between the bursts of reproduction.

Many annual plants, by contrast, are semelparous: they have a sudden burst of flowering and seed set, and then they die. This is commonly the case among the weeds of arable crops. Others, such as groundsel, are iteroparous: they continue to grow and produce new flowers and seeds through the season until they are killed by the first lethal frost of winter. They die with their buds on.

seed banks

Most annuals spend part of the year dormant as seeds, spores, cysts or eggs. In many cases these dormant stages may remain viable for many years; there are reliable records of seeds of the annual weeds *Chenopodium album* and *Spergula arvensis* remaining viable in soil for 1600 years. Similarly, the dried eggs of brine shrimps remain viable for many years in storage. This means that if we measure the length of life from the time of formation of the zygote, many so-called ‘annual’ animals and plants live very much longer than a single year. Large populations of dormant seeds form a *seed bank* buried in the soil: as many as 86,000 viable seeds per square meter have been found in cultivated soils. The species composition of the seed bank may be very different from that of the mature vegetation above it (Figure 5.6). Species of annuals that seem to have become locally extinct may suddenly reappear after the soil is disturbed and these seeds germinate.

ephemeral ‘annuals’ of deserts

Dormant seeds, spores or cysts are also necessary to the many ephemeral plants and animals of sand dunes and deserts that complete most of their life cycle in less than 8 weeks. They then depend on the dormant stage to persist through the remainder of the year and survive the hazards of low temperatures in winter and the droughts of summer. In desert environments, in fact, the rare rains are not

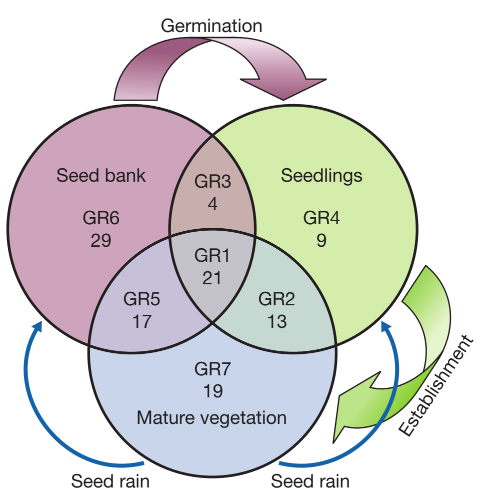
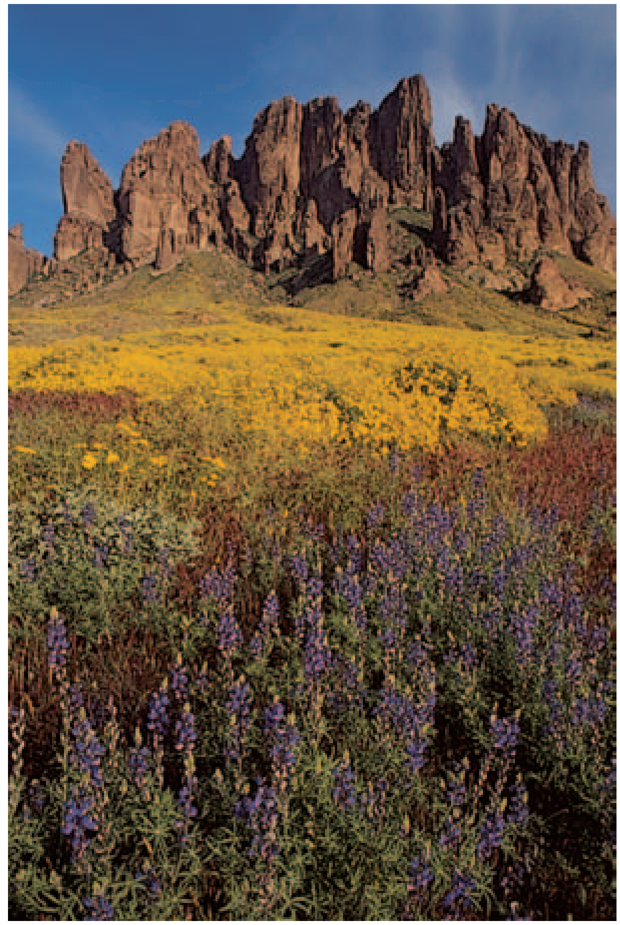


Figure 5.6

Species recovered from the seed bank, from seedlings and from the mature vegetation in a coastal grassland site on the western coast of Finland. Species may germinate from the buried seed bank into seedlings, and seedlings may establish themselves in the mature vegetation. Mature plants may contribute seeds (in the ‘seed rain’) that germinate into seedlings immediately or enter the buried seed bank. Seven species groups (GR1–GR7) are defined on the basis of whether they were found in only one, two or all three life stages. The marked difference in composition, especially between the seed bank and the mature vegetation, is readily apparent. Thirty-two species in the mature vegetation (19 + 13) were not represented in the seed bank; 33 species in the seed bank were not found in the mature vegetation, and 29 of these were not found as seedlings either.



A desert in bloom. In desert areas where rainfall is rare and seasonally unpredictable, a dense and spectacular flora of very short-lived annuals commonly develops after rain storms. They often complete their life cycle from germination to seed set in little more than a month.

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necessarily seasonal, and it is only in occasional years that sufficient rain falls and stimulates the germination of characteristic and colorful floras of very small ephemeral plants.

5.2.3 Longer life cycles

repeated, seasonal breeders

There is a marked seasonal rhythm in the lives of many long-lived plants and animals, especially in their reproductive activity: a period of reproduction once per year (Figure 5.7a). Mating (or the flowering of plants) is commonly triggered by the length of the *photoperiod* – the light phase in the daily light–dark cycle, which varies continuously through the year – and usually makes sure that young are born, eggs hatch or seeds are ripened when seasonal resources are likely to be abundant.

In populations of perennial species, the generations overlap and individuals of a range of ages breed side by side. The population is maintained in part by survival of adults and in part by new births. A study of the great tit *Parus major*, for example, showed that of 50 eggs that were laid by a breeding population of 10 birds in one season, only 30 hatchlings survived to become fully fledged, and

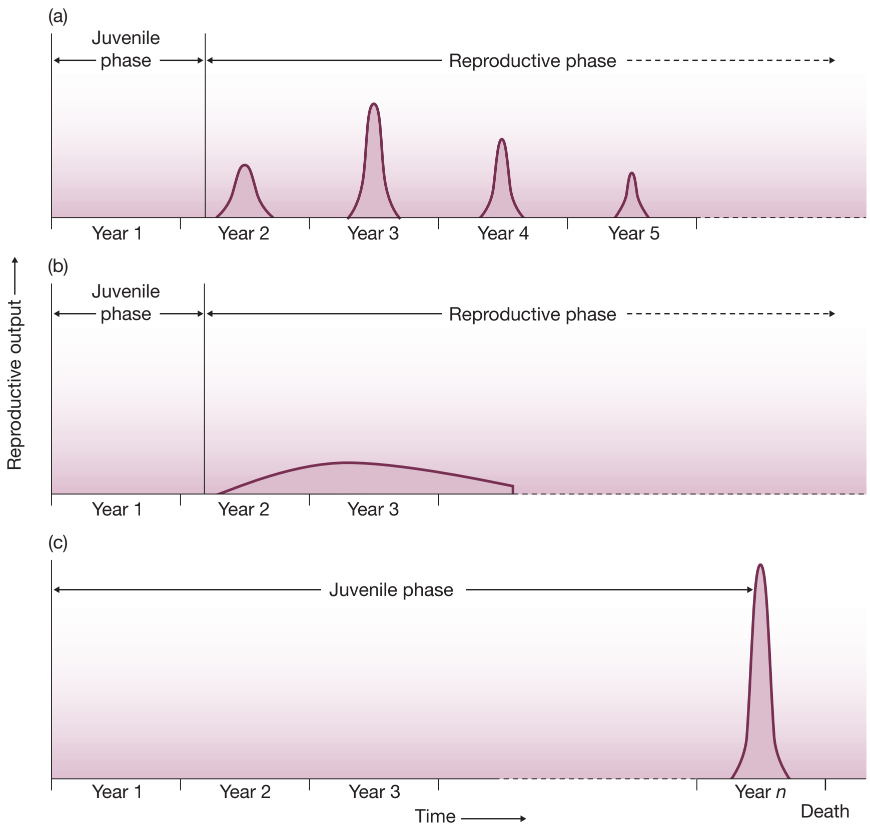


Figure 5.7
Simplified life histories for organisms living more than 1 year. (a) An iteroparous species breeding seasonally once per year. Death tends not to occur predictably after any given time, though a decline toward senescence is often observed. (b) An iteroparous species breeding continuously throughout the year. The pattern of death and decline is similar to that in (a). (c) A semelparous species passing several or many years in a pre-reproductive juvenile phase, followed by a burst of reproduction, followed in turn by inevitable death.

only three of these survived to adulthood the following year. These three 1-year-old birds were joined in that second year, though, by a further five birds aged between 2 and 5 years – the survivors of the previous year's 10 (Figure 5.8).

continuous breeders

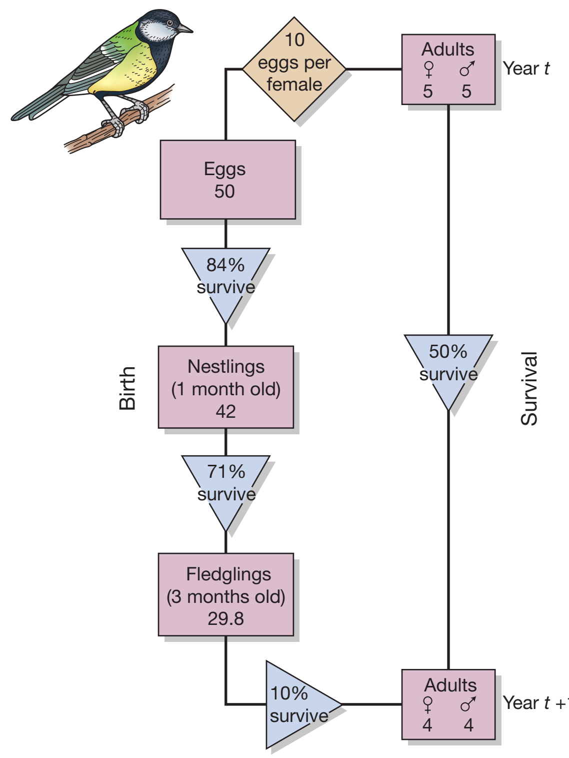
In wet equatorial regions, on the other hand, where there is very little seasonal variation in temperature and rainfall and scarcely any variation in photoperiod, we find species of plant that are in flower and fruit throughout the year – and continuously breeding species of animal that subsist on this resource (Figure 5.7b). There are several species of fig (*Ficus*), for instance, that bear fruit continuously and form a reliable year-round food supply for birds and primates. In more seasonal climates, humans are unusual in also breeding continuously throughout the year, though numbers of other species, cockroaches for example, do so in the stable environments that humans have created.

semelparous species like salmon and bamboo

Other plants and animals (Figure 5.7c) may spend almost all their lives in a long non-reproductive (juvenile) phase and then have one lethal burst of reproductive activity. We saw such semelparity earlier in biennial plants, but it is also characteristic of some species that live much longer than 2 years. The Pacific salmon is a familiar example. Salmon are spawned in rivers. They spend the first phase of their juvenile life in fresh water and then migrate to the sea, often traveling thousands of miles. At maturity they return to the stream in which they were hatched. Some mature and return to reproduce after only 2 years at sea; others mature more slowly and return after 3, 4 or 5 years. At the time of

Figure 5.8

A diagrammatic life history for a population of great tits near Oxford, UK. Individuals typically live for several years; hence, the population in any one year is a combination of survivors from previous years and newborn individuals. Population sizes (in rectangles) are per hectare; the proportions surviving from one stage to the next are in triangles; the rate of egg production per female is shown in the diamond.



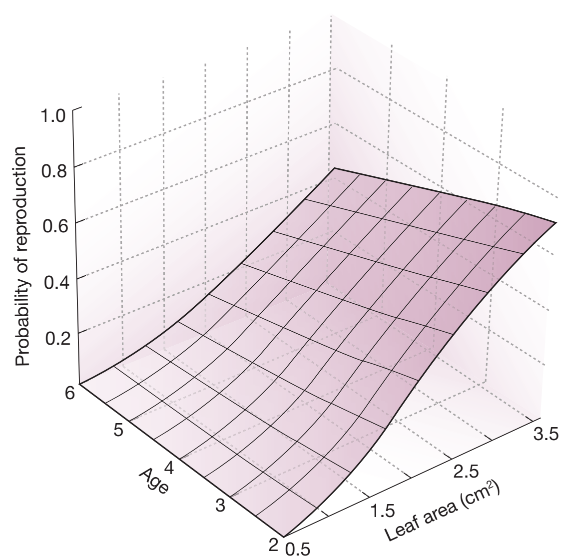
AFTER PERRINS, 1965

reproduction, the population of salmon is composed of overlapping generations of individuals. But all are semelparous: they lay their eggs and then die; their bout of reproduction is terminal.

There are even more dramatic examples of species that have a long life but reproduce just once. Many species of bamboo form dense clones of shoots that

Figure 5.9

The effect of plant age (years) and plant size (as measured by leaf area) on the probability of *Rhododendron lapponicum* shoots entering their reproductive phase. The relationships have been 'smoothed' by a statistical technique called 'logistic regression'. Note that the probability of reproduction increases with plant size at all ages. Also, older shoots are overall more likely to enter their reproductive phase because they tend to be bigger. However, at any given size, the probability of reproduction tends to *decrease* with age, making age itself a much poorer predictor of shoot fate than size.



AFTER KARLSSON & JACOBSON, 2001

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.

size matters

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.

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

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