

rather than growing longer). Conversely, the rate of growth of populations can be slowed by delaying the onset of reproduction. One very effective way in which the growth rate of human populations can be slowed down, for example (see Chapter 12), is by discouraging early marriage and childbearing.

We can now turn to the life history patterns themselves. The potential of a species to multiply rapidly is advantageous in environments that are short-lived, allowing the organisms to colonize new habitats quickly and exploit new resources. This rapid multiplication is a characteristic of the life cycles of terrestrial organisms that invade disturbed land (for example, many annual weeds), or colonize newly opened habitats such as forest clearings, and of the aquatic inhabitants of temporary puddles and ponds. These are species whose populations are usually found expanding after the last disaster or exploiting the new opportunity. They have the life cycle properties that are favored by natural selection in such conditions: the production of large numbers of progeny, early in the life cycle, rather than investing heavily in either growth or survival. They have been called *r* species, because they spend most of their life in the near-exponential, *r*-dominated phase of population growth (see Box 5.4), and the habitats in which they are likely to be favored have been called *r*-selecting.

Organisms with quite different life histories survive in habitats where there is often intense competition for limited resources. The individuals that are successful in leaving descendants are those that have captured, and often held on to, the larger share of resources. Their populations are usually crowded and those that win in a struggle for existence do so because they have grown faster and/or larger (rather than reproducing) or have spent more of their resources in aggression or some other activity that has favored their survival under crowded conditions. They are called *K* species because their populations spend most of their lives in the *K*-dominated phase of population growth (see Box 5.4) – ‘bumping up’ against the limits of environmental resources – and the habitats in which they are likely to be favored have been called *K*-selecting.

A further common distinction between *r* and *K* species is whether they produce many small progeny (characteristic of *r* species) or few large progeny (characteristic of *K* species). This is another example of a life history trade-off: an organism has limited resources available for reproduction, and natural selection will influence how these are packaged. In environments where rapid population growth is possible, those individuals that produce large numbers of small progeny will be favored. The size of progeny can be sacrificed because they will usually not be in competition with others. However, in environments in which the individuals are crowded and there is competition for resources, those progeny that are well provided with resources by the parent will be favored. Producing progeny that are well endowed requires the trade-off of producing fewer of them (see, for example, Figure 5.28).

The *r/K* concept can certainly be useful in describing some of the general differences among different organisms. For instance, among plants it is possible to describe a number of very broad and general relationships (Figure 5.29). Trees in a forest are splendid examples of *K* species. They compete for light in the canopy, and survivors are those that put their resources into early growth and overtopping their neighbors. They usually delay reproduction until their branches have an assured place in the canopy of leaves. Once established they hold on to their position and usually have a very long life, with a relatively low allocation

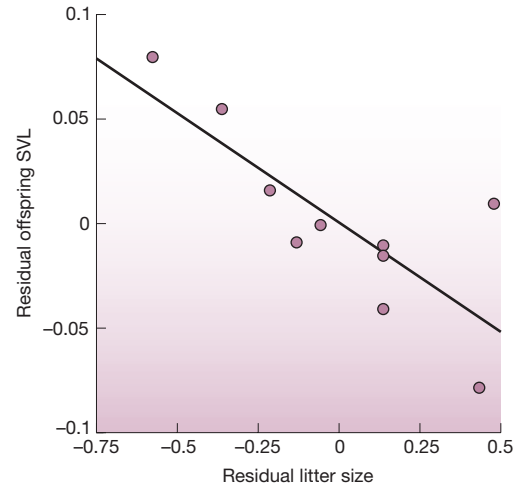
r and *K* species

r, *K* and progeny size and number

evidence for the *r/K* scheme?

Figure 5.28

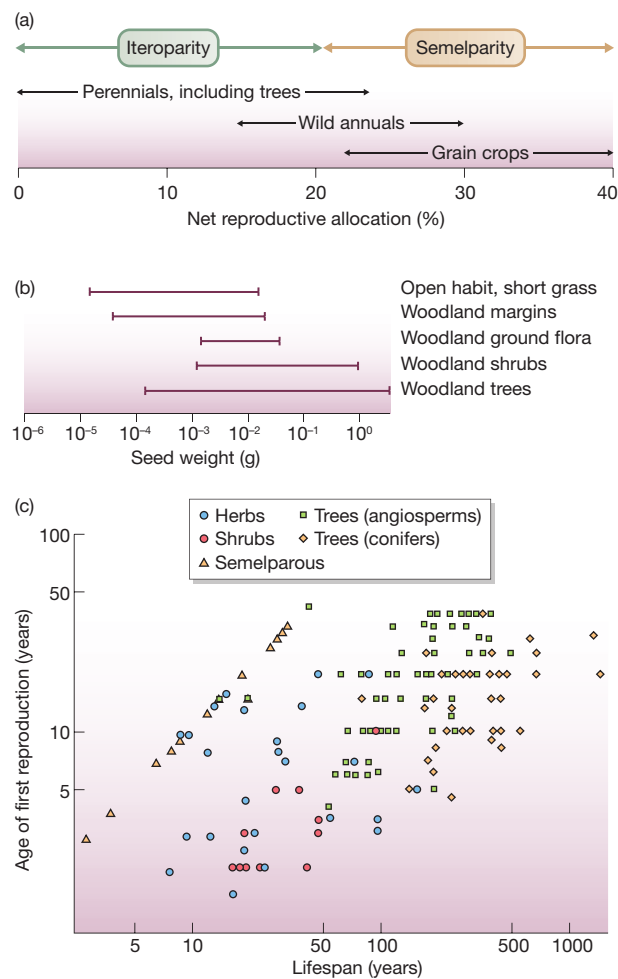
Evidence for a trade-off between the number of offspring produced in a clutch by a parent and the individual fitness of those offspring: a negative correlation between the size of offspring (as measured by their snout–vent length, SVL) and the number of them in a litter in the Australian highland copperhead snake, *Austrelaps ramsayi* ($r^2 = 0.63$, $P = 0.006$). 'Residual' offspring and litter sizes have been used: these are the values arrived at after variations in maternal size have been allowed for, since both increase with maternal size.



AFTER ROHR, 2001

Figure 5.29

Broadly speaking, plants show some conformity with the r/K scheme. For example, trees in relatively K -selecting woodland habitats: (a) have a relatively high probability of being iteroparous and a relatively small reproductive allocation; (b) have relatively large seeds; and (c) are relatively long-lived with relatively delayed reproduction.



AFTER HARPER, 1977; FROM SALISBURY, 1942; OGDEN, 1968; HARPER & WHITE, 1974

to reproduction overall but large individual seeds. By contrast, in more disturbed, open, r -selecting habitats, the plants tend to conform to the general syndrome of r characteristics: a greater reproductive allocation, but smaller seeds, smaller size, earlier reproduction and a shorter life (Figure 5.29).

On the other hand, there seem to be about as many examples that fail to fit the r/K scheme as examples that correspond. One might regard this as a damning criticism of the r/K concept, since it undoubtedly demonstrates that the explanatory powers of the scheme are limited. But it is equally possible to regard it as very satisfactory that a relatively simple concept can help make sense of a large proportion of the multiplicity of life histories. Nobody, though, can regard the r/K scheme as the whole story. Like all attempts to classify species and their characteristics into pigeonholes, the distinction between r and K species has to be recognized as a convenient (and useful) human creation rather than an all-encompassing statement about the living world.



Summary

Counting individuals, births and deaths

Ecologists try to describe and understand the distribution and abundance of organisms. The processes that change the size of populations are birth, death and movement. A population is a number of individuals, but for some kinds of organism, especially modular organisms, it is not always clear what we mean by an individual.

Ecologists face enormous problems when they try to count what is happening to populations in nature. They almost always estimate rather than count. There are particular problems in counting modular organisms and the numbers of births and deaths.

Life cycles and reproduction

The life histories of all unitary organisms can be seen as variations around a simple, sequential pattern. Some organisms fit several or many generations within a single year, some breed predictably just once each year (annuals), and others (perennials) have a life cycle extended over several or many years. Some, iteroparous species, breed repeatedly; others, semelparous species, have a single reproductive episode followed quickly by death.

Most annuals germinate or hatch in spring, grow rapidly, reproduce and then die before the end of summer. Most spend part of the year dormant. There is a marked seasonal rhythm in the lives of many long-lived species. Where there is very little seasonal variation, some reproduce throughout the year; others have a long non-reproductive phase and then one lethal burst of reproductive activity.

Monitoring birth and death: life tables and fecundity schedules

Life tables can be useful in identifying what in a life cycle is apparently most instrumental in determining rates of increase or decline. A cohort life table records the survivorship of members of a single cohort. When we cannot follow cohorts, it may be possible to construct a static life table, but great care is required. The fecundity of individuals also changes with age, described in age-specific fecundity schedules.

Ecologists search for patterns of life and death that we can see repeated in the lives of many species. A useful set of survivorship curves (types I–III) has been developed, but in practice patterns of survival are usually more complex.

Dispersal and migration

Dispersal is the way individuals spread away from each other. Migration is the mass directional movement of large numbers of a species from one location to another. Movement and spatial distribution are intimately related. Dispersal and migration can have a profound effect on the dynamics of a population and on its composition.

The impact of intraspecific competition on populations

Over a sufficiently large density range, competition between individuals generally reduces the birth rate as density increases and increases the death rate (i.e. is density-dependent). Intraspecific competition therefore tends to keep density within certain limits and may thus be said to play a part in regulating the size of populations.

When populations are sparse and uncrowded they tend to exhibit exponential growth, but the rate of increase tends to become reduced by competition as the population grows, giving rise to population growth that is not exponential but S-shaped or logistic.

Intraspecific competition also affects net recruitment, typically resulting in a humped curve.

Life history patterns

There is typically a limited total amount of energy or some other resource available to an organism for growth and reproduction. There may be an observable cost of reproduction. But populations of individuals that reproduce early in their life can grow extremely fast.

The potential of a species to multiply rapidly is favored by natural selection in environments that are short-lived, allowing the organisms to colonize new habitats quickly and exploit new resources. Such species have been called *r* species. Where there is often intense competition for limited resources, the individuals that are successful in leaving descendants are those that have captured the larger share of resources, often because they were born larger and/or have grown faster (rather than reproducing): so-called *K* species. The *r/K* concept can be useful in interpreting many of the differences in form and behavior of organisms, but of course it is not the whole story.

Review questions

REVIEW QUESTIONS

Asterisks indicate challenge questions

- 1 Contrast the meaning of the word 'individual' for unitary and modular organisms.
- 2 In a mark-recapture exercise during which a population of butterflies remained constant in size, an initial sample provided 70 individuals, each of which was marked and then released back into the population. Two days later, a second sample was taken, totaling 123 individuals of which 47 bore a mark from the first sample. Estimate the size of the population. State any assumptions that you have had to make in arriving at your estimate.
- 3* Define annual, perennial, semelparous and iteroparous. Try to give an example of both an animal and a plant for each of the four possible combinations of these terms. In which cases is it difficult (or impossible) to come up with an example and why?
- 4 Contrast the derivation of cohort and static life tables and discuss the problems of constructing and/or interpreting each.
- 5 The following is an outline life table and fecundity schedule for a cohort of a population of sparrows. Fill in the missing values (wherever there is a question mark).