

**Figure 4.4 Integration within a plant leads to a shifting balance of positive and negative effects between parent and daughter modules as modules age.** The growth of daughter ramets of the grass *Holcus lanatus*, which were initially (a) one week, (b) two weeks, (c) four weeks and (d) eight weeks old, and were then grown on for a further eight weeks. LSD, least significant difference, needs to be exceeded for two means to be significantly different from each other. For further discussion, see text. CC, competing, connected; CN, competing, not connected; NN, independent plants, neither competing nor connected. *Source:* After Bullock *et al.* (1994).

with their consequences – the total number of individuals present and the way these numbers vary with time. Whether organisms are unitary or modular, ecologists face enormous technical problems when they try to count what is happening to populations in nature. A great many ecological questions remain unanswered because of these problems.

#### what is a population?

It is usual to use the term *population* to describe a group of individuals of one species under investigation.

What actually constitutes a population, though, will vary from species to species and from study to study. In some cases, the boundaries of a population are readily apparent: the sticklebacks occupying a small lake are ‘the stickleback population of the lake’. In other cases, boundaries are determined more by an investigator’s purpose or convenience: it is possible to study the population of lime aphids inhabiting one leaf, one tree, one stand of trees or a whole woodland. In yet other cases – and there are many of these – individuals are distributed continuously over a wide area, and an investigator must define the limits of a population arbitrarily. In such cases, especially, it is often more convenient to consider the *density* of a population. This is usually defined as ‘numbers per unit area’, but in certain circumstances ‘numbers per leaf’, ‘numbers per host’ or some other measure may be appropriate.

#### estimating population size

To determine the size of a population, one might imagine that it is possible simply to count individuals, especially for relatively small, isolated habitats like islands and relatively large individuals like deer. For most species, however, such ‘complete enumerations’ are impractical or impossible: observability – our ability to observe every individual

present – is almost always less than 100%. Ecologists, therefore, must almost always *estimate* the number of individuals in a population rather than count them. They may estimate the numbers of aphids on a crop, for example, by counting the number on a representative sample of leaves, then estimating the number of leaves per square metre of ground, and from this estimating the number of aphids per square metre. For plants and animals living on the ground surface, the sample unit is generally a small area known as a quadrat (which is also the name given to the square or rectangular device used to demarcate the boundaries of the area on the ground). For soil-dwelling organisms the unit is usually a volume of soil; for lake dwellers a volume of water; for many herbivorous insects the unit is one typical plant or leaf, and so on. Further details of sampling methods, and of methods for counting individuals generally, can be found in one of many texts devoted to ecological methodology (e.g. Krebs, 1999; Henderson & Southwood, 2016).

For animals, especially, there are two further methods of estimating population size. The first is known as *capture-recapture*. At its simplest, this involves catching a random sample of a population, marking individuals so that they can be recognised subsequently, releasing them so that they remix with the rest of the population, and then catching a further random sample. Population size can be estimated from the proportion of this second sample that bear a mark, since, as long as the population remains the same between the two samples, that proportion should be the same as in the whole population, and the number marked in the population is known, since we, the investigators, marked and released them. In practice, there is usually a whole sequence of capture-recapture samples (not just two), and the

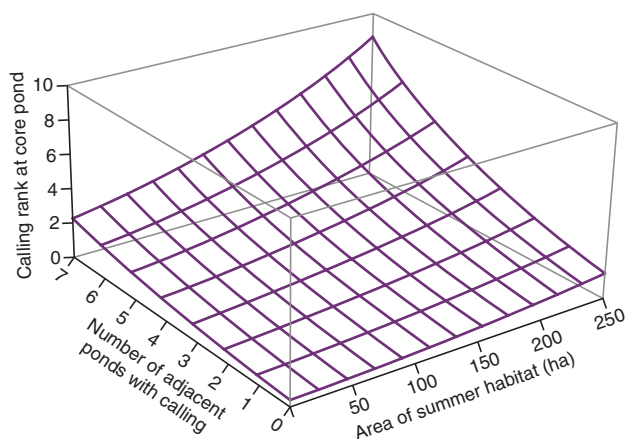
assumption that populations remain the same between samples is relaxed. Methods of analysis are consequently more complex and more powerful (Cooch & White, 2019).

The final method is to use an *index of abundance*. This can provide information on the relative size of a population, but by itself usually gives little indication of absolute size. As an example, Figure 4.5 shows how the number of occupied ponds, and the amount of summer (terrestrial) habitat in the vicinity of a pond, affected the abundance of leopard frogs (*Rana pipiens*) near Ottawa, Canada. Here, frog abundance was estimated from the ‘calling rank’, based on 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.

#### counting births

Counting births can be more difficult even than counting individuals.

The formation of the zygote is often regarded as the starting point in the life of an individual. But it is a stage that is often hidden and extremely hard to study. We simply do not know, for most animals and plants, how many embryos die before ‘birth’, though in the rabbit at least 50% of embryos are thought to die in the womb, and in many higher plants it seems that about 50% of embryos abort before the seed is fully grown and mature. Hence, it is almost always impossible in practice to treat the start of life as the time of birth. In birds we may use the moment that an egg hatches; in mammals, perhaps, when



**Figure 4.5 Indices of abundance can provide valuable information.** The abundance (calling rank) of leopard frogs 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. Source: After Pope *et al.* (2000).

an individual starts to be supported outside the mother as a suckling; and in plants we may use the germination of a seed as the birth of a seedling, although it is really only the moment at which a developed embryo restarts into growth after a period of dormancy. We need to remember that often half or more of a population will have died before they can be recorded as born!

Counting deaths poses as many problems. Dead bodies do not linger long in nature. Only the skeletons of large animals persist long after death. Seedlings may be counted and mapped one day and gone without trace the next. Mice, voles and soft-bodied animals such as caterpillars and worms are digested by predators or rapidly removed by scavengers or decomposers. They leave no carcasses to be counted and no evidence of the cause of death. Capture–recapture methods can go a long way towards estimating deaths from the loss of marked individuals from a population (they are probably used as often to measure survival as abundance), but even here it is often impossible to distinguish loss through death and loss through emigration.

#### counting deaths

## 4.4 Life cycles

We have noted already that counting the numbers in a population provides only an outline sketch, and one key reason for this is that virtually all organisms go through a number of stages in their lives, each with their own birth and death rates, responses to other organisms, resources and conditions, and so on. Hence, we need to understand the sequences of events that occur in those organisms’ life cycles. A highly simplified, generalised life history is outlined in Figure 4.6a. It comprises birth, followed by a prereproductive period, a period of reproduction, perhaps a postreproductive period, and then death as a result of senescence (though of course other forms of mortality may intervene at any time). The variety of life cycles is also summarised diagrammatically in Figure 4.6, although there are many life cycles that defy this simple classification. Some organisms fit several or many generations within a single year, some have just one generation each year (annuals), and others 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.

Whatever the length of their life cycle, species may, broadly, be either *semelparous* or *iteroparous* (often referred to by plant scientists

#### semelparous and iteroparous life cycles