

# Chapter 5

## Intraspecific Competition

### 5.1 Introduction

Organisms grow, reproduce and die (Chapter 4). They are affected by the conditions in which they live (Chapter 2), and by the resources that they obtain (Chapter 3). But no organism lives in isolation. Each, for at least part of its life, is a member of a population composed of individuals of its own species.

#### a definition of competition

Individuals of the same species have very similar requirements for survival, growth and reproduction; but their combined demand for a resource may exceed the immediate supply. The individuals then compete for the resource and, not surprisingly, at least some of them become deprived. This chapter is concerned with the nature of such intraspecific competition, its effects on the competing individuals and on populations of competing individuals. We begin with a working definition: 'competition is an interaction between individuals, brought about by a shared requirement for a resource, and leading to a reduction in the survivorship, growth and/or reproduction of at least some of the competing individuals concerned'. We can now look more closely at competition.

Consider, initially, a simple hypothetical community: a thriving population of grasshoppers (all of one species) feeding on a field of grass (also of one species). To provide themselves with energy and material for growth and reproduction, grasshoppers eat grass; but in order to find and consume that grass they must use energy. Any grasshopper might find itself at a spot where there is no grass because some other grasshopper has eaten it. The grasshopper must then move on and expend more energy before it takes in food. The more grasshoppers there are, the more often this will happen. An increased energy expenditure and a decreased rate of food intake may all decrease a grasshopper's chances of survival, and also leave less energy available for development and reproduction. Survival and reproduction determine a grasshopper's contribution to the next generation. Hence, the

more intraspecific competitors for food a grasshopper has, the less its likely contribution will be.

As far as the grass itself is concerned, an isolated seedling in fertile soil may have a very high chance of surviving to reproductive maturity. It will probably exhibit an extensive amount of modular growth, and will probably therefore eventually produce a large number of seeds. However, a seedling that is closely surrounded by neighbors (shading it with their leaves and depleting the water and nutrients of its soil with their roots) will be very unlikely to survive, and if it does, will almost certainly form few modules and set few seeds.

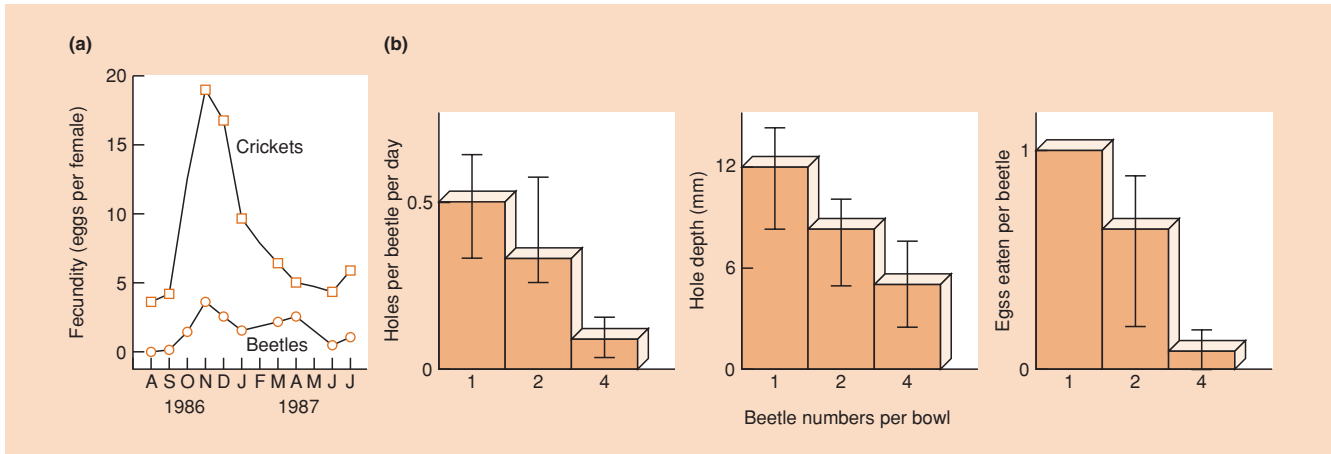
We can see immediately that the ultimate effect of competition on an individual is a decreased contribution to the next generation compared with what would have happened had there been no competitors. Intraspecific competition typically leads to decreased rates of resource intake per individual, and thus to decreased rates of individual growth or development, or perhaps to decreases in the amounts of stored reserves or to increased risks of predation. These may lead, in turn, to decreases in survivorship and/or decreases in fecundity, which together determine an individual's reproductive output.

#### 5.1.1 Exploitation and interference

In many cases, competing individuals do not interact with one another directly.

#### exploitation

Instead, individuals respond to the level of a resource, which has been depressed by the presence and activity of other individuals. The grasshoppers were one example. Similarly, a competing grass plant is adversely affected by the presence of close neighbors, because the zone from which it extracts resources (light, water, nutrients) has been overlapped by the 'resource depletion zones' of these neighbors, making it more difficult to extract those resources. In such cases, competition may be described as



**Figure 5.1** Intraspecific competition amongst cave beetles (*Neapheanops tellkampfi*). (a) Exploitation. Beetle fecundity is significantly correlated ( $r = 0.86$ ) with cricket fecundity (itself a good measure of the availability of cricket eggs – the beetles' food). The beetles themselves reduce the density of cricket eggs. (b) Interference. As beetle density in experimental arenas with 10 cricket eggs increased from 1 to 2 to 4, individual beetles dug fewer and shallower holes in search of their food, and ultimately ate much less ( $P < 0.001$  in each case), in spite of the fact that 10 cricket eggs was sufficient to satiate them all. Means and standard deviations are given in each case. (After Griffith & Poulson, 1993.)

*exploitation*, in that each individual is affected by the amount of resource that remains after that resource has been exploited by others. Exploitation can only occur, therefore, if the resource in question is in limited supply.

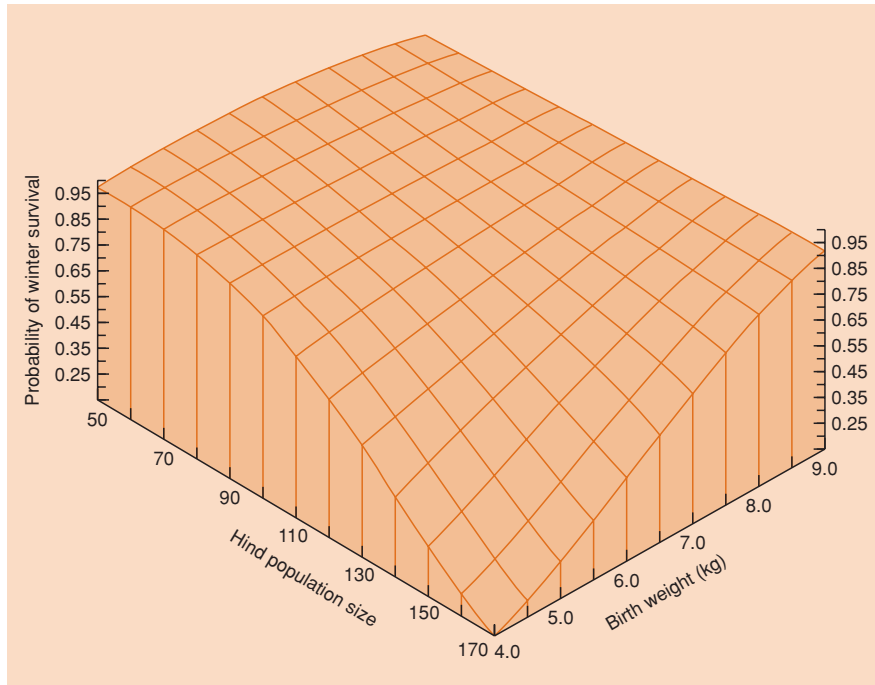
In many other cases, competition takes the form of *interference*. Here individuals interact directly with each other, and one individual will actually prevent another from exploiting the resources within a portion of the habitat. For instance, this is seen amongst animals that defend territories (see Section 5.11) and amongst the sessile animals and plants that live on rocky shores. The presence of a barnacle on a rock prevents any other barnacle from occupying that same position, even though the supply of food at that position may exceed the requirements of several barnacles. In such cases, space can be seen as a resource in limited supply. Another type of interference competition occurs when, for instance, two red deer stags fight for access to a harem of hinds. Either stag, alone, could readily mate with all the hinds, but they cannot both do so since matings are limited to the 'owner' of the harem.

Thus, interference competition may occur for a resource of real value (e.g. space on a rocky shore for a barnacle), in which case the interference is accompanied by a degree of exploitation, or for a surrogate resource (a territory, or ownership of a harem), which is only valuable because of the access it provides to a real resource (food, or females). With exploitation, the intensity of competition is closely linked to the level of resource present and the level required, but with interference, intensity may be high even when the level of the real resource is not limiting.

In practice, many examples of competition probably include elements of both exploitation and interference. For instance, adult cave beetles, *Neapheanops tellkampfi*, in Great Onyx Cave, Kentucky, compete amongst themselves but with no other species and have only one type of food – cricket eggs, which they obtain by digging holes in the sandy floor of the cave. On the one hand, they suffer indirectly from exploitation: beetles reduce the density of their resource (cricket eggs) and then have markedly lower fecundity when food availability is low (Figure 5.1a). But they also suffer directly from interference: at higher beetle densities they fight more, forage less, dig fewer and shallower holes and eat far fewer eggs than could be accounted for by food depletion alone (Figure 5.1b).

### 5.1.2 One-sided competition

Whether they compete through exploitation or interference, individuals within a species have many fundamental features in common, using similar resources and reacting in much the same way to conditions. None the less, intraspecific competition may be very one sided: a strong, early seedling will shade a stunted, late one; an older and larger bryozoan on the shore will grow over a smaller and younger one. One example is shown in Figure 5.2. The overwinter survival of red deer calves in the resource-limited population on the island of Rhum, Scotland (see Chapter 4) declined sharply as the population became more crowded, but those that were smallest at birth were by far the most likely to die. Hence, the ultimate effect of competition is



**Figure 5.2** Those red deer that are smallest when born are the least likely to survive over winter when, at higher densities, survival declines. (After Clutton-Brock *et al.*, 1987.)

far from being the same for every individual. Weak competitors may make only a small contribution to the next generation, or no contribution at all. Strong competitors may have their contribution only negligibly affected.

Finally, note that the likely effect of intraspecific competition on any individual is greater the more competitors there are. The effects of intraspecific competition are thus said to be density dependent. We turn next to a more detailed look at the density-dependent effects of intraspecific competition on death, birth and growth.

## 5.2 Intraspecific competition, and density-dependent mortality and fecundity

Figure 5.3 shows the pattern of mortality in the flour beetle *Tribolium confusum* when cohorts were reared at a range of densities. Known numbers of eggs were placed in glass tubes with 0.5 g of a flour–yeast mixture, and the number of individuals that survived to become adults in each tube was noted. The same data have been expressed in three ways, and in each case the resultant curve has been divided into three regions. Figure 5.3a describes the relationship between density and the *per capita* mortality rate – literally, the mortality rate ‘per head’, i.e. the probability of an individual dying or the proportion that died between the egg and adult stages. Figure 5.3b describes how the number that died prior to the adult stage changed with density; and Figure 5.3c describes the relationship between density and the numbers that survived.

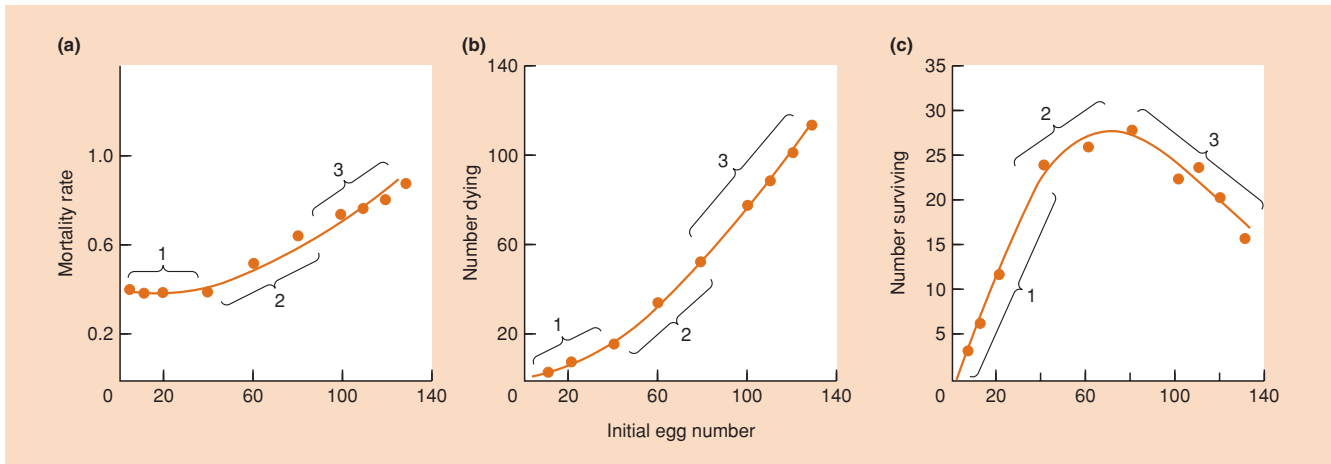
Throughout region 1 (low density) the mortality rate remained constant as density was increased (Figure 5.3a). The numbers dying and the numbers surviving both rose (Figure 5.3b, c) (not surprising, given that the numbers ‘available’ to die and survive increased), but the proportion dying remained the same, which accounts for the straight lines in region 1 of these figures. Mortality in this region is said to be density independent. Individuals died, but the chance of an individual surviving to become an adult was not changed by the initial density. Judged by this, there was no intraspecific competition between the beetles at these densities. Such density-independent deaths affect the population at all densities. They represent a baseline, which any density-dependent mortality will exceed.

In region 2, the mortality rate increased with density (Figure 5.3a): there was density-dependent mortality. The numbers dying continued to rise with density, but unlike region 1 they did so more than proportionately (Figure 5.3b). The numbers surviving also continued to rise, but this time less than proportionately (Figure 5.3c). Thus, over this range, increases in egg density continued to lead to increases in the total number of surviving adults. The mortality rate had increased, but it ‘undercompensated’ for increases in density.

undercompensating  
density dependence

In region 3, intraspecific competition was even more intense. The increasing mortality rate ‘overcompensated’ for any increase in density, i.e. over this range, the more eggs there were present, the fewer adults survived: an increase in the initial number of eggs led to an even

overcompensating  
density dependence

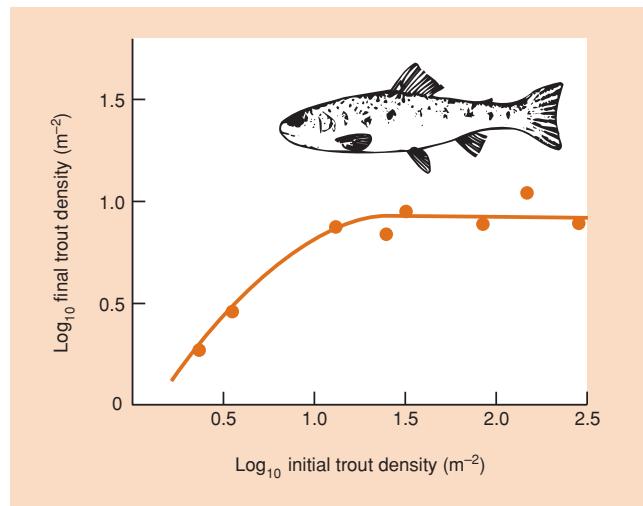


**Figure 5.3** Density-dependent mortality in the flour beetle *Tribolium confusum*: (a) as it affects mortality rate, (b) as it affects the numbers dying, and (c) as it affects the numbers surviving. In region 1 mortality is density independent; in region 2 there is undercompensating density-dependent mortality; in region 3 there is overcompensating density-dependent mortality. (After Bellows, 1981.)

greater proportional increase in the mortality rate. Indeed, if the range of densities had been extended, there would have been tubes with no survivors: the developing beetles would have eaten all the available food before any of them reached the adult stage.

**exactly compensating density dependence**

A slightly different situation is shown in Figure 5.4. This illustrates the relationship between density and mortality in young trout. At the lower densities there was undercompensating density dependence, but at higher densities mortality never overcompensated. Rather, it compensated exactly for any increase in density: any rise in the number of fry was matched by an exactly equivalent rise in the



**Figure 5.4** An exactly compensating density-dependent effect on mortality: the number of surviving trout fry is independent of initial density at higher densities. (After Le Cren, 1973.)

mortality rate. The number of survivors therefore approached and maintained a constant level, irrespective of initial density.

The patterns of density-dependent fecundity that result from intraspecific competition are, in a sense, a mirror-image of those for mortality (Figure 5.5).

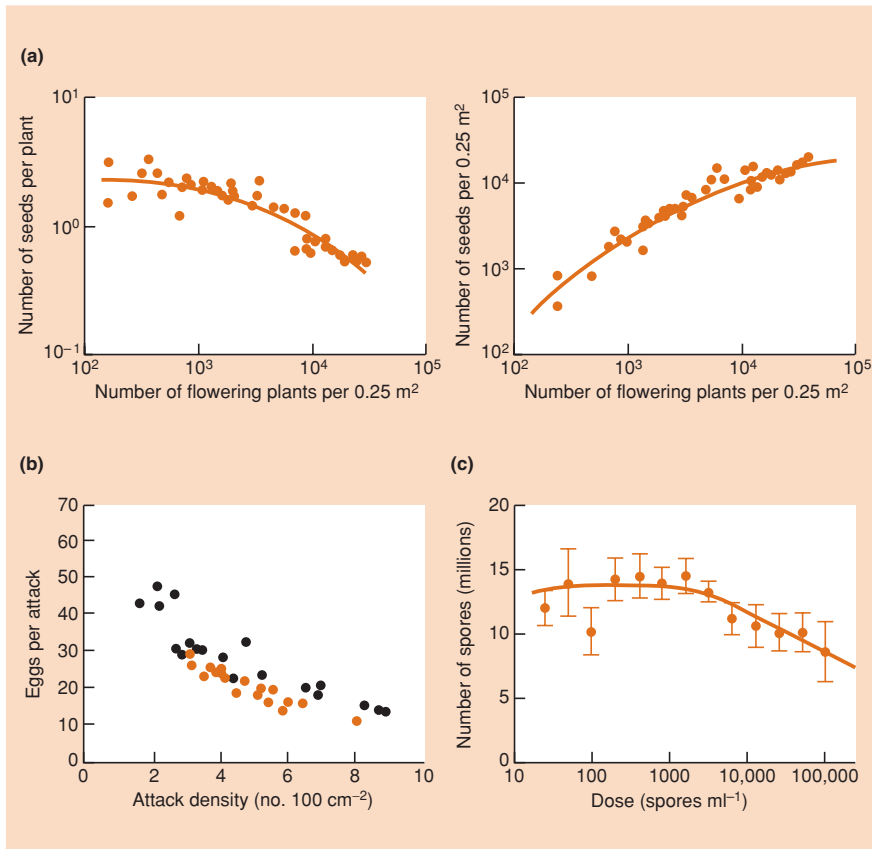
**intraspecific competition and fecundity**

Here, though, the per capita birth rate falls as intraspecific competition intensifies. At low enough densities, the birth rate may be density independent (Figure 5.5a, lower densities). But as density increases, and the effects of intraspecific competition become apparent, birth rate initially shows undercompensating density dependence (Figure 5.5a, higher densities), and may then show exactly compensating density dependence (Figure 5.5b, throughout; Figure 5.5c, lower densities) or overcompensating density dependence (Figure 5.5c, higher densities).

Thus, to summarize, irrespective of variations in over- and undercompensation, the essential point is a simple one: at appropriate densities, intraspecific competition can lead to density-dependent mortality and/or fecundity, which means that the death rate increases and/or the birth rate decreases as density increases. Thus, whenever there is intraspecific competition, its effect, whether on survival, fecundity or a combination of the two, is density dependent. However, as subsequent chapters will show, there are processes other than intraspecific competition that also have density-dependent effects.

### 5.3 Density or crowding?

Of course, the intensity of intraspecific competition experienced by an individual is not really determined by the density of the population as a whole. The effect on an individual is determined,



**Figure 5.5** (a) The fecundity (seeds per plant) of the annual dune plant *Vulpia fasciculata* is constant at the lowest densities (density independence, left). However, at higher densities, fecundity declines but in an undercompensating fashion, such that the total number of seeds continues to rise (right). (After Watkinson & Harper, 1978.) (b) Fecundity (eggs per attack) in the southern pine beetle, *Dendroctonus frontalis*, in East Texas declines with increasing attack density in a way that compensates more or less exactly for the density increases: the total number of eggs produced was roughly 100 per 100 cm<sup>2</sup>, irrespective of attack density over the range observed (●, 1992; ●, 1993). (After Reeve *et al.*, 1998.) (c) When the planktonic crustacean *Daphnia magna* was infected with varying numbers of spores of the bacterium *Pasteuria ramosa*, the total number of spores produced per host in the next generation was independent of density (exactly compensating) at the lower densities, but declined with increasing density (overcompensating) at the higher densities. Standard errors are shown. (After Ebert *et al.*, 2000.)

rather, by the extent to which it is crowded or inhibited by its immediate neighbors.

One way of emphasizing this is by noting that there are actually at least three different meanings of ‘density’ (see Lewontin & Levins, 1989, where details of calculations and terms can be found). Consider a population of insects, distributed over a population of plants on which they feed. This is a typical example of a very general phenomenon – a population (the insects in this case) being distributed amongst different patches of a resource (the plants). The density would usually be calculated as the number of insects (let us say 1000) divided by the number of plants (say 100), i.e. 10 insects per plant. This, which we would normally call simply the ‘density’, is actually the ‘resource-weighted density’. However, it gives an accurate measure of the intensity of competition suffered by the insects (the extent to which they are crowded) only if there are exactly 10 insects on every plant and every plant is the same size.

#### three meanings of density

Suppose, instead, that 10 of the plants support 91 insects each, and the remaining 90 support just one insect.

The resource-weighted density would still be 10 insects per plant. But the average density experienced by the insects would be 82.9 insects per plant. That is, one adds

up the densities experienced by each of the insects (91 + 91 + 91 . . . + 1 + 1) and divides by the total number of insects. This is the ‘organism-weighted density’, and it clearly gives a much more satisfactory measure of the intensity of competition the insects are likely to suffer.

However, there remains the further question of the average density of insects experienced by the plants. This, which may be referred to as the ‘exploitation pressure’, comes out at 1.1 insects per plant, reflecting the fact that most of the plants support only one insect.

What, then, is the density of the insect? Clearly, it depends on whether you answer from the perspective of the insect or the plant – but whichever way you look at it, the normal practice of calculating the resource-weighted density and calling it the ‘density’ looks highly suspect. The difference between resource- and organism-weighted densities is illustrated for the human population of a number of US states in Table 5.1 (where the ‘resource’ is simply land area). The organism-weighted densities are so much larger than the usual, but rather unhelpful, resource-weighted densities essentially because most people live, crowded, in cities (Lewontin & Levins, 1989).

The difficulties of relying on density to characterize the potential intensity of intraspecific competition are particularly

**Table 5.1** A comparison of the resource- and organism-weighted densities of five states, based on the 1960 USA census, where the ‘resource patches’ are the counties within each state. (After Lewontin & Levins, 1989.)

State	Resource-weighted density (km <sup>-2</sup> )	Organism-weighted density (km <sup>-2</sup> )
Colorado	44	6,252
Missouri	159	6,525
New York	896	48,714
Utah	28	684
Virginia	207	13,824

acute with sessile, modular organisms, because, being sessile, they compete almost entirely only with their immediate neighbors, and being modular, competition is directed most at the modules that are closest to those neighbors. Thus, for instance, when silver birch

trees (*Betula pendula*) were grown in small groups, the sides of individual trees that interfaced with neighbors typically had a lower ‘birth’ and higher death rate of buds (see Section 4.2); whereas on sides of the same trees with no interference, bud birth rate was higher, death rate lower, branches were longer and the form approached that of an open-grown individual (Figure 5.6). Different modules experience different intensities of competition, and quoting the density at which an individual was growing would be all but pointless.

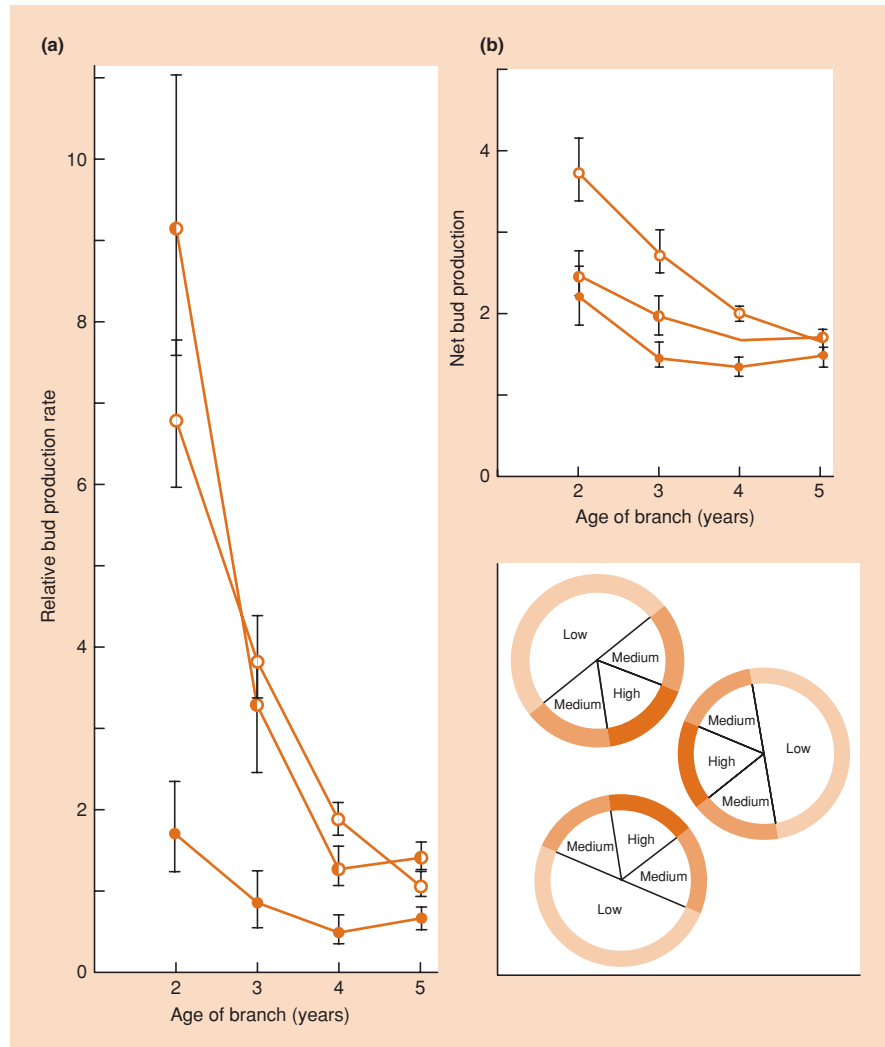
Thus, whether mobile or sessile, different individuals meet or suffer from different numbers of competitors.

density: a convenient expression of crowding

Density, especially resource-weighted

density, is an abstraction that applies to the population as a whole but need not apply to any of the individuals within it. None the less, density may often be the most convenient way of expressing the degree to which individuals are crowded – and it is certainly the way it has usually been expressed.

**Figure 5.6** Mean relative bud production (new buds per existing bud) for silver birch trees (*Betula pendula*), expressed (a) as gross bud production and (b) as net bud production (birth minus death), in different interference zones. These zones are themselves explained in the inset. ●, high interference; ○, medium; ○, low. Bars represent standard errors. (After Jones & Harper, 1987.)

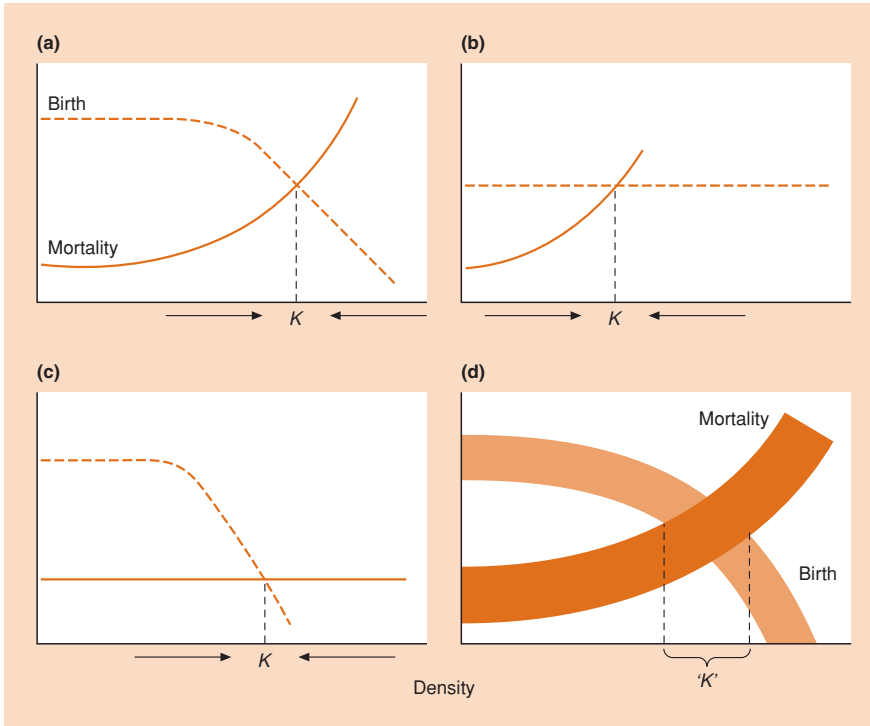


**5.4 Intraspecific competition and the regulation of population size**

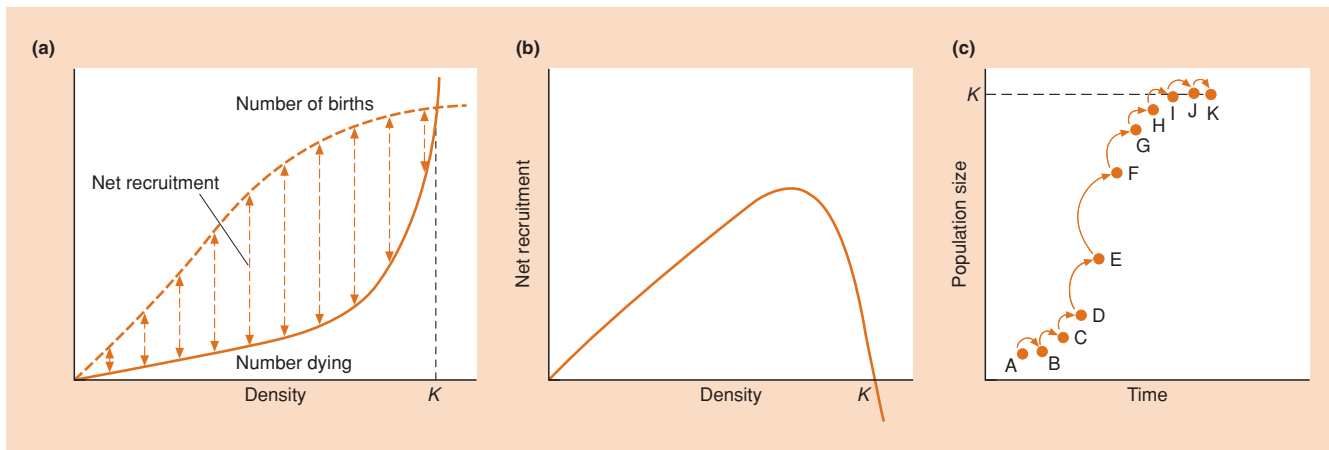
There are, then, typical patterns in the effects of intraspecific competition on birth and death (see Figures 5.3–5.5). These generalized patterns are summarized in Figures 5.7 and 5.8.

**5.4.1 Carrying capacities**

Figure 5.7a–c reiterates the fact that as density increases, the per capita birth rate eventually falls and the per capita death rate eventually rises. There must, therefore, be a density at which these curves cross. At densities below this point, the birth rate exceeds



**Figure 5.7** Density-dependent birth and mortality rates lead to the regulation of population size. When both are density dependent (a), or when either of them is (b, c), their two curves cross. The density at which they do so is called the carrying capacity ( $K$ ). Below this the population increases, above it the population decreases:  $K$  is a stable equilibrium. However, these figures are the grossest of caricatures. The situation is closer to that shown in (d), where mortality rate broadly increases, and birth rate broadly decreases, with density. It is possible, therefore, for the two rates to balance not at just one density, but over a broad range of densities, and it is towards this broad range that other densities tend to move.



**Figure 5.8** Some general aspects of intraspecific competition. (a) Density-dependent effects on the numbers dying and the number of births in a population: net recruitment is ‘births minus deaths’. Hence, as shown in (b), the density-dependent effect of intraspecific competition on net recruitment is a domed or ‘n’-shaped curve. (c) A population increasing in size under the influence of the relationships in (a) and (b). Each arrow represents the change in size of the population over one interval of time. Change (i.e. net recruitment) is small when density is low (i.e. at small population sizes: A to B, B to C) and is small close to the carrying capacity (I to J, J to K), but is large at intermediate densities (E to F). The result is an ‘S’-shaped or sigmoidal pattern of population increase, approaching the carrying capacity.

the death rate and the population increases in size. At densities above the crossover point, the death rate exceeds the birth rate and the population declines. At the crossover density itself, the two rates are equal and there is no net change in population size. This density therefore represents a stable equilibrium, in that all other densities will tend to approach it. In other words, intraspecific competition, by acting on birth rates and death rates, can regulate populations at a stable density at which the birth rate equals the death rate. This density is known as the *carrying capacity* of the population and is usually denoted by  $K$  (Figure 5.7). It is called a carrying capacity because it represents the population size that the resources of the environment can just maintain ('carry') without a tendency to either increase or decrease.

real populations lack simple carrying capacities

However, whilst hypothetical populations caricatured by line drawings like Figures 5.7a–c can be characterized by a simple carrying capacity, this is not true of any natural population. There are unpredictable environmental fluctuations; individuals are affected by a whole wealth of factors of which intraspecific

competition is only one; and resources not only affect density but respond to density as well. Hence, the situation is likely to be closer to that depicted in Figure 5.7d. Intraspecific competition does not hold natural populations to a predictable and unchanging level (the carrying capacity), but it may act upon a very wide range of starting densities and bring them to a much narrower range of final densities, and it therefore tends to keep density within certain limits. It is in this sense that intraspecific competition may be said typically to be capable of regulating population size. For instance, Figure 5.9 shows the fluctuations within and between years in populations of the brown trout (*Salmo trutta*) and the grasshopper, *Chorthippus brunneus*. There are no simple carrying capacities in these examples, but there are clear tendencies for the 'final' density each year ('late summer numbers' in the first case, 'adults' in the second) to be relatively constant, despite the large fluctuations in density within each year and the obvious potential for increase that both populations possess.

In fact, the concept of a population settling at a stable carrying capacity, even in caricatured populations, is relevant only to situations in which density dependence is not strongly overcompensating. Where there is overcompensation, cycles or even

**Figure 5.9** Population regulation in practice. (a) Brown trout (*Salmo trutta*) in an English Lake District stream.  $\Delta$ , numbers in early summer, including those newly hatched from eggs;  $\circ$ , numbers in late summer. Note the difference in vertical scales. (After Elliott, 1984.) (b) The grasshopper, *Chorthippus brunneus*, in southern England.  $\bullet$ , eggs;  $+$ , nymphs;  $\circ$ , adults. Note the logarithmic scale. (After Richards & Waloff, 1954.) There are no definitive carrying capacities, but the 'final' densities each year ('late summer' and 'adults') are relatively constant despite large fluctuations within years.

