

5.8.3 Asymmetry enhances regulation

One final, important general point is that these asymmetries tend to reinforce the regulatory powers of intraspecific competition, in much the same way as exactly-compensating or 'contest' competition (Section 5.3) gives rise to the most tightly regulated populations. This can be seen especially in a much longer term study that will almost certainly never be repeated, where a population of the herbaceous perennial, *Anemone hepatica*, in Sweden was visited and revisited every year from 1943 to 1956, with each plant being tracked individually (Figure 5.30; Tamm, 1956). Crops of seedlings entered the population each year between 1943 and 1952, but nonetheless, the most important factor determining which individuals survived to 1956 was whether or not they were established in 1943. Of the 30 individuals that were already of a large or intermediate size in 1943, 28 survived until 1956, and some of these had branched. By contrast, of the 112 plants that were either small in 1943 or appeared as seedlings subsequently, only 26 survived to 1956, and not one of these was sufficiently well established to have flowered. Tamm's established plants were successful competitors – winners in a contest – year after year, but his small plants and seedlings were repeatedly unsuccessful. This guaranteed a near constancy in the number of established, winning plants between 1943 and 1956, accompanied by a variable number of 'losers' that not only failed to grow, but usually, in due course, died. Similar patterns can be observed in tree populations. The survival rates, the birth rates and thus the fitnesses of the few established adults are high; those of the many seedlings and saplings are low.

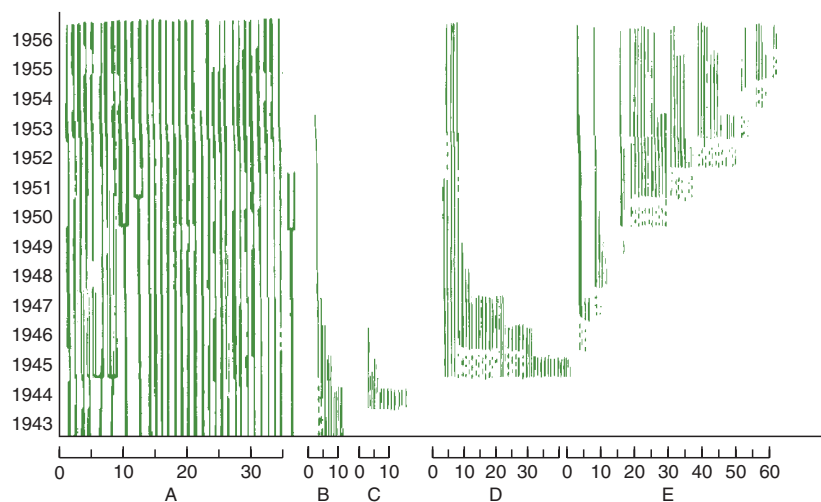
5.8.4 Territoriality

Territoriality refers to active interference between individuals, such that a more or less exclusive area, the territory, is defended against intruders by a recognizable pattern of behaviour. It is one widespread and important example of asymmetric intraspecific competition.

Individuals of a territorial species that fail to obtain a territory, commonly referred to as 'floaters', often make no contribution whatsoever to future generations. Territoriality, therefore, is a 'contest'. There are winners (those that come to hold a territory) and losers (those that do not), and at any one time there can be only a limited number of winners. The exact number of territories (winners) in a population may vary, depending on resources or environmental conditions. We see this, for example, for the number of tawny owl (*Strix aluco*) territories in a Finnish population, and especially the number of productive territories, which varies with the abundance of their vole prey (Figure 5.31). Nonetheless, the contest nature of territoriality ensures, like asymmetric competition generally, a comparative constancy in the number of surviving, reproducing individuals. In the past, some felt that these regulatory consequences of territoriality must themselves be the root cause underlying the evolution of territorial behaviour – territoriality being favoured because the population as a whole benefitted from the rationing effects, which guaranteed that the population did not overexploit its resources (e.g. Wynne-Edwards, 1962). However, there are powerful and

territoriality is a contest and regulates population size

Figure 5.30 Asymmetric competition enhances population size regulation in an anemone. Space pre-emption in a perennial, *Anemone hepatica*, in a Swedish forest. Each line represents one individual: straight for unramified ones, branched where the plant has ramified (i.e. produced new plants by vegetative growth), bold where the plant flowered and broken where the plant was not seen that year. Group A were alive and large in 1943, group B alive and small in 1943, group C appeared first in 1944, group D in 1945 and group E thereafter, presumably from seedlings. Source: After Tamm (1956).



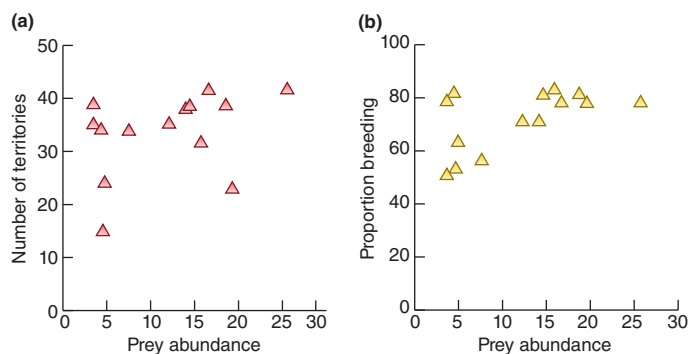


Figure 5.31 The number of (successful) territories may increase at higher resource levels. (a) The number of territories occupied by tawny owls, *Strix aluco*, in a study in Finland tends to increase as the abundance of their vole prey increases, though not significantly, but (b) the proportion of these in which territory holders are successful in breeding increases significantly with prey abundance ($P = 0.007$). Source: After Karell *et al.* (2009).

fundamental reasons for rejecting this ‘group selectionist’ explanation (essentially, it stretches evolutionary theory beyond reasonable limits): the ultimate cause of territoriality must be sought within the realms of natural selection, in some advantage accruing to the individuals concerned.

benefits and costs of territoriality

Any benefit that an individual does gain from territoriality, of course, must be set against the costs of defending the territory. In some animals this defence involves fierce combat between competitors, while in others there is a more subtle mutual recognition by competitors of one another’s keep-out signals (e.g. song or scent). Even when the chances of physical injury are minimal, territorial animals typically expend energy in marking, patrolling and advertising their territories. Hence, for territoriality to be favoured by natural selection, we expect the benefits to exceed these costs. Indeed, we expect territories to be an optimum size – ‘as large as necessary but as small as possible’ (Kittle *et al.*, 2015) – in that as territory size increases, defence costs will also increase but resource access is increasingly likely to exceed the animals’ requirements. This in turn suggests that as habitat quality (and resource ‘concentration’) increases, territory sizes should decrease (they do not need to be as large), which is precisely what we see for the lion territories in Figure 5.32.

floater? or territory holder?

On the other hand, explaining territoriality only in terms of a net benefit to the territory owner is rather like history always being written by the victors. A trickier question, which has received less attention, asks to what extent floaters, without a territory, are simply losers or are themselves net beneficiaries of a strategy they have adopted. Three main hypotheses, not mutually exclusive and all receiving some support, have been proposed for what determines whether an individual, as a result of a contest, becomes a floater or a

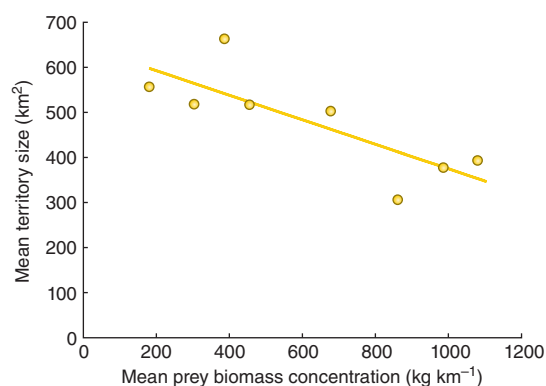


Figure 5.32 Territory sizes occupied by male lions (*Panthera leo*) in Zimbabwe decreased as habitat quality increased. Habitat quality was equated with the estimated concentration of the biomass of a wide range of prey species. Source: After Loveridge *et al.* (2015).

territory holder: (i) territory holders are in some sense ‘stronger’, (ii) they have skills that they have acquired with age, and (iii) they are winners because they have acquired familiarity, as holders of the territory already (Sergio *et al.*, 2009). Variants of these hypotheses also include there being a ‘convention’, respected by the participants, through which the larger animal or the territory holder *always* wins. There is no doubt that some floaters are simply losers: too small, too young or too lacking in local knowledge, and therefore *en route* to dying without making any contribution to future generations. However, we see in Figure 5.33, for example, that for black kites, *Milvus migrans*, in the Doñana National Park in Spain, where floaters are neither smaller, nor in worse condition, and there is no ‘resident always wins’ rule, floaters are predominantly the youngest individuals, and territory holders are all members of the older age classes. Hence, for many of these floaters, it is not so much a case of reproduction-denied as reproduction-deferred. It therefore makes evolutionary sense for the

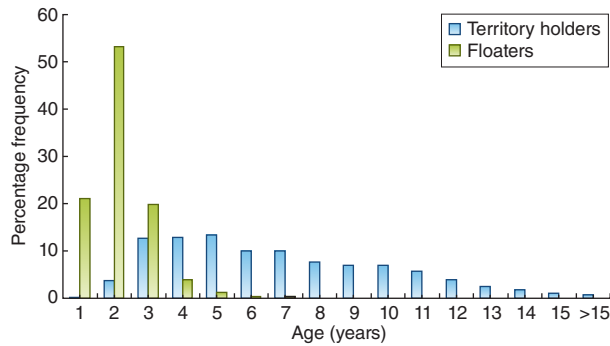


Figure 5.33 Older individuals hold the territories in a black kite population. The age profile of territory holders and non-territory holding floaters in a black kite, *Milvus migrans*, population in the Doñana National Park in Spain. Source: After Sergio *et al.* (2009).

young floaters to invest little in territorial contests in their earliest years (and in that sense ‘accept’ their floater status, temporarily) so as to maximise their chances of surviving long enough to win a territory later.

dear enemies and nasty neighbours

The idea that territorial strategies will be favoured that minimise costs to the territory holders also implies that the territory holders should, where possible, tailor their level of effort to the level of threat being posed. This has led to two contrasting hypotheses. The ‘dear enemy’ hypothesis proposes that more effort should be exerted against strangers unfamiliar to the territory holder, lacking territories themselves, than against territory-holding neighbours, since, once a territorial boundary has been established, it pays both neighbours to minimise their investment in maintaining it (Fisher, 1954). But on the other hand, the ‘nasty neighbour’ hypothesis proposes that more aggression should be displayed against neighbours than strangers, and proposes it especially for group-living species, where out-competing your neighbour allows your group to swell in size (Temeles, 1994). There is evidence for both (Figure 5.34), and while the dear enemy effect seen for the rodents in Figure 5.34a appears to be the more common, the nasty neighbour effect does indeed appear to be most often found in group-living species, such as the ants in Figure 5.34b.

5.9 Self-thinning

We have seen throughout this chapter that intraspecific competition can influence the number of deaths, the number of births and the amount of growth within a population.

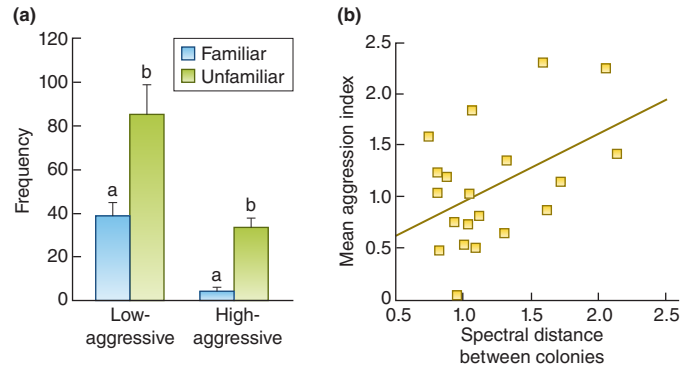


Figure 5.34 ‘Dear enemy’ and ‘nasty neighbour’ effects.

(a) Male subterranean rodents, *Ctenomys talarum* (tuco-tucos) in Argentina display more aggressive (especially high-aggressive) behaviour towards unfamiliar than towards familiar opponents in staged contest. Familiarity was gained by previously exposing contestants to the odour of their opponents. In the ‘unfamiliar’ treatment, exposure was to an odour of an animal other than the opponent. Bars are SEs; different letters denote significant differences ($P < 0.05$). (b) Weaver ant colonies, *Oecophylla smaragdina*, in Queensland, Australia, behaved more aggressively towards other colonies the less related they were to them in terms of the chemicals in their cuticle (less related = greater ‘spectral distance’). Source: (a) After Zenuto (2010). (b) After Newey *et al.* (2010).

We have illustrated this largely by looking at the end results of competition. But in practice the effects are often progressive. As a cohort ages, the individuals grow in size, their requirements increase, and they therefore compete at a greater and greater intensity. This in turn tends to increase their risk of dying. But if some individuals die, then the density is decreased as is the intensity of competition – which affects growth, which affects competition, which affects survival, which affects density, and so on.

In trying to understand these interconnected processes it is important to distinguish three types of study: (i) those in which the ‘final’ performance of competitors is monitored over a range of densities and hence over a range of intensities of competition; (ii) those in which density and performance are monitored together over time as groups of competitors grow and undergo density-dependent mortality; and (iii) those which seek relationships between density and performance in sets of populations, each observed just once (Weiner & Freckleton, 2010). Each type of study involves density and the performance of either individual competitors or the whole population, but the three tend to be aimed at addressing rather different questions. We

APPLICATION 5.3 Reintroduction of territorial vultures

Having seen that many species compete for territories related to the availability of resources rather than for the resources themselves, it is perhaps not surprising that when we come to manage such species, ensuring the availability of territories is a top priority. A good example comes from a study of bearded vultures, *Gypaetus barbatus*, which became extinct in the European Alps more than a century ago, and have been the focus of a reintroduction programme since 1986 (Figure 5.35). Captive-reared individuals were released from four widely dispersed sites from which they spread to new areas, and this spread was monitored in the Valais region of Switzerland (not one of the release sites). During an initial phase, from 1987 to 1994, the sightings were of subadults, and the most

important factor explaining the distribution of these sightings was the biomass of ibex, *Capra ibex*, whose carcasses are an important resource for the vultures. However, during the subsequent phase, from 1995 to 2001, when adults were finally settling in the region, the presence of the vultures was most closely correlated with the distribution of craggy limestone crags, which are the ideal base for their territories, providing nest sites, thermal conditions for soaring, and limestone screes for bone breaking and food storage. Food availability was of only secondary significance. It seems clear, therefore, that future reintroductions in the area should focus precisely on the availability of these viable territories.

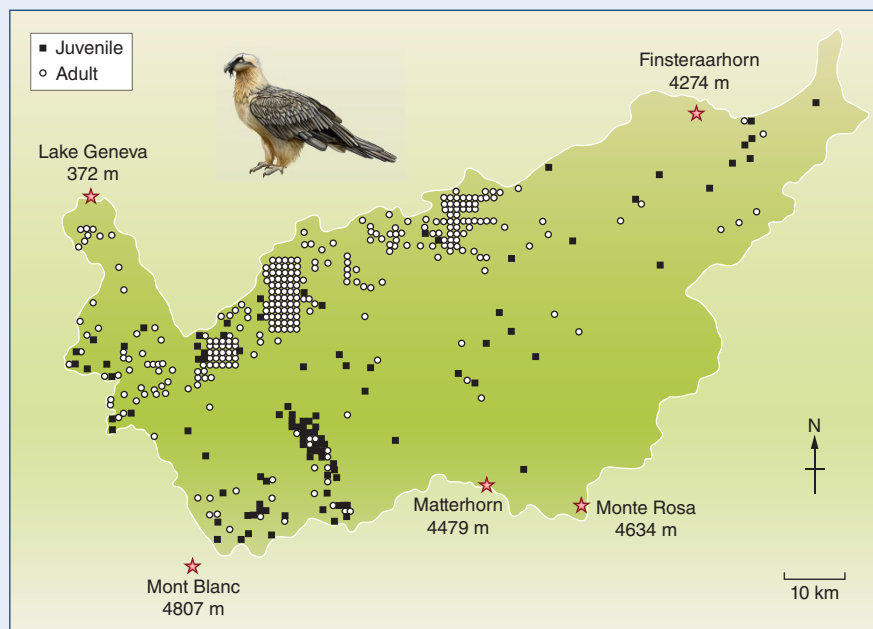


Figure 5.35 The importance of good territories for the conservation of bearded vultures. Map of the Valais region of Switzerland, where bearded vultures, *Gypaetus barbatus*, have spread following their reintroduction. Black squares are 1 km squares where juvenile vultures were sighted during an initial, 'prospecting' stage (1987–94). White circles are 1 km squares where adult vultures were sighted during a subsequent, 'settling' stage (1995–2001). Source: After Hirzel *et al.* (2004).

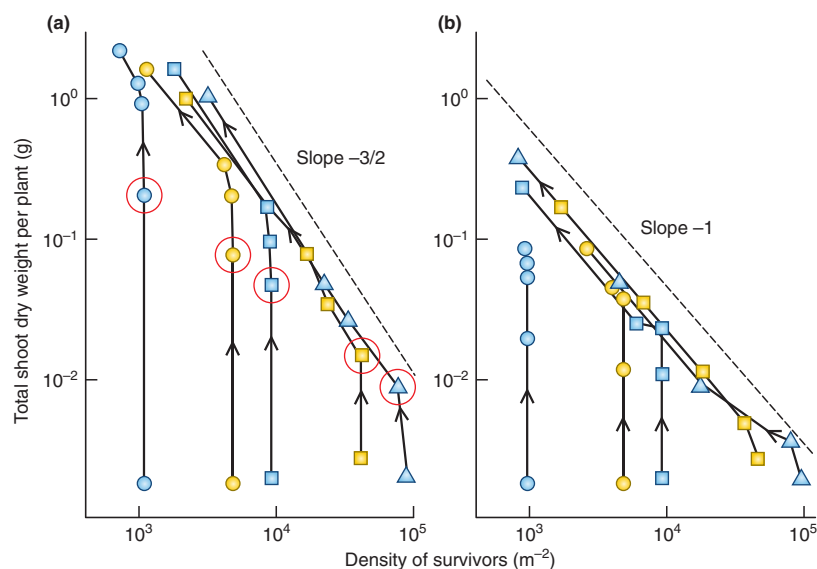
examined the first in Section 5.2.2 when we discussed constant final yield. We turn here to the second and third.

5.9.1 Dynamic thinning lines

Starting with the second, the patterns that emerge in growing, crowded cohorts of individuals were originally the focus of particular attention in plant populations. For

example, perennial rye grass (*Lolium perenne*) was sown at a range of densities, and samples from each density were harvested after 14, 35, 76, 104 and 146 days (Figure 5.36a). Figure 5.36a has the same logarithmic axes – density and mean plant weight – as Figure 5.7: what we referred to previously as a type (i) study. In Figure 5.7, each line represented a separate yield–density relationship at different ages of a cohort, and the points along a line represented different initial sowing densities. In Figure 5.36, on

Figure 5.36 Crowded plant populations typically approach and then track self-thinning lines. Self-thinning in *Lolium perenne* sown at five densities: 1000 (○), 5000 (●), 10 000 (■), 50 000 (□) and 100 000 (△) 'seeds' m⁻², in (a) 0% shade, where the observations after 35 days are circled in red, and (b) 83% shade. The lines join populations of the five sowing densities harvested on five successive occasions. They therefore indicate the trajectories, over time, that these populations would have followed. The arrows indicate the directions of the trajectories, i.e. the direction of self-thinning. For further discussion, see text. Source: After Lonsdale & Watkinson (1983).



the other hand, each line itself represents a different initial density and successive points along a line represent populations at different ages. Each line is therefore a trajectory that follows a cohort through time, as indicated by the arrows in Figure 5.36, pointing from many small, young individuals (bottom right) to fewer, larger, older individuals (top left).

We can see that mean plant weight at a given age was always greatest in the lowest density populations (illustrated, for example, after 35 days (circled points) in Figure 5.36a). It is also clear that the highest density populations were the first to suffer substantial mortality. What is most noticeable, though, is that eventually, in all cohorts, density declined and mean plant weight increased in unison: populations progressed along roughly the *same* straight line. The populations are said to have experienced *self-thinning* (i.e. a progressive decline in density in a population of growing individuals), and the line that they approached and then followed is known as a *dynamic thinning line* (Weller, 1990).

The lower the sowing density, the later was the onset of self-thinning. In all cases, though, the populations initially followed a trajectory that was almost vertical, reflecting the fact that there was little mortality. Then, as they neared the thinning line, the populations suffered increasing amounts of mortality, so that the slopes of all the self-thinning trajectories gradually approached the dynamic thinning line and then progressed along it. Note also that Figure 5.36 has been drawn, following convention, with log density on the *x*-axis and log mean weight on the *y*-axis. This is not meant to imply that density is the independent variable on which mean weight depends. Indeed, it can be argued that the truth is the reverse of this: that mean weight

increases naturally during plant growth, and this determines the decrease in density. The most satisfactory view is that density and mean weight are wholly interdependent.

Plant populations (if sown at sufficiently high densities) have repeatedly been found to approach and then follow a dynamic thinning line. For many years, all such lines were widely perceived as having a slope of roughly $-3/2$, and the relationship was often referred to as the ' $-3/2$ power law' (Yoda *et al.*, 1963; Hutchings, 1983), since density (N) was seen as related to mean weight (\bar{w}) by the equation:

$$\log \bar{w} = \log c - 3/2 \log N \quad (5.22)$$

or:

$$\bar{w} = cN^{-3/2} \quad (5.23)$$

where c is constant. (In fact, as we shall see, this is even further from being a universal law than the 'law' of constant final yield, discussed previously.)

Note, however, that there are statistical problems in using Equations 5.22 and 5.23 to estimate the slope of the relationship in that \bar{w} is usually estimated as B/N , where B is the total biomass per unit area, and so \bar{w} and N are inevitably correlated, and any relationship between them is, to a degree, spurious (Weller, 1987). It is therefore preferable to use the equivalent relationships relating overall biomass to density, lacking autocorrelation:

$$\log B = \log c - 1/2 \log N \quad (5.24)$$

or:

$$B = cN^{-1/2}. \quad (5.25)$$