Chapter 6. Living in Groups

Show anyone 10 000 flamingos nesting beak by jowl in a colony and the chances are that sooner or later they will ask 'Why on earth are they all nesting so close together?'. In this chapter we will look at why animals live in groups: why flamingos flock, horses herd and sardines shoal. Using the methods described in Chapter 2 (comparison between or within species and experimental studies of costs and benefits) we will show how ecological pressures might favour living in groups.

Food and predators influence the costs and benefits of group living

Comparisons between species suggest that the two main environmental influences on group size are food and predators (Chapter 2) and comparisons between populations within a species also emphasize their importance (Fig. 6.1). In many studies either costs or benefits related to feeding and predation have been measured and we will describe some of these in the first part of the chapter, before moving on to consider whether different kinds of cost and benefit can be combined to predict optimal group size. Animals which do not live in groups (and also some which do) often defend resources from which they exclude other members of the same species. Therefore the question 'Why live in a group?' is a natural complement to the question 'Why defend resources?' that we discussed in Chapter 5.

Living in groups and avoiding predation

The guppies in Fig. 6.1a live in groups when they are in streams where predators are common, which suggests that being in a group might help an individual to avoid becoming a meal. This could happen in several different ways.

INCREASED VIGILANCE

Many eyes are better than one

For many predators success depends on surprise: if the victim is alerted too soon during an attack, the predator's chance of success is low. This is true, for example, of goshawks hunting for pigeon flocks (Fig. 6.2). The hawks are less successful in attacks on large flocks of pigeons mainly because the birds in a large flock take to the air when the hawk is still some distance away. If each pigeon in the flock occasionally looks up to scan for a hawk, the bigger the flock the more likely it is that one bird will be alert when the hawk looms over the horizon. Once one pigeon takes off the others follow at once.

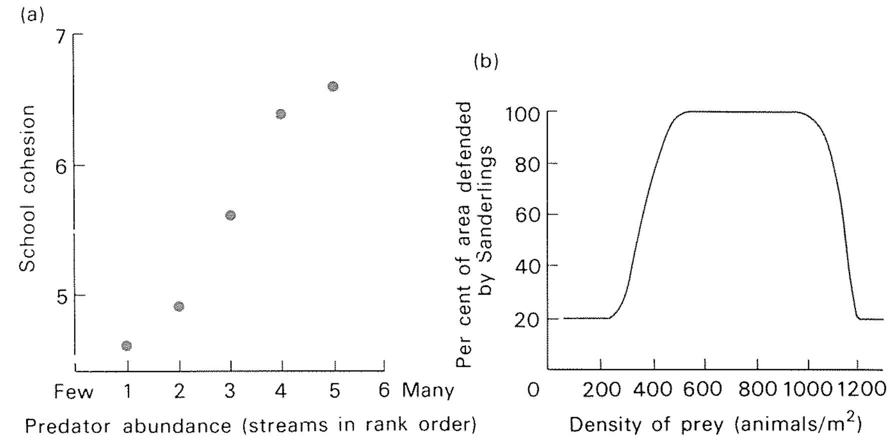

Fig. 6.1 Intraspecific variation in group size may be related to predators and food. (a) Guppies (*Poecilia reticulata*) from different streams in Trinidad: guppies from streams with many predators live in tighter schools than those from streams with few predators. Each dot is a different stream and 'cohesion' was measured by counting the number of fish in grid squares on the bottom of a tank. From Seghers (1974). (b) Sanderlings (*Calidris alba*) in Bodega Bay, California. The birds defend stretches of beach in some parts of the intertidal zone and feed in roving flocks on other parts of the beach. Whether or not the birds defend territories depends on the density of the major prey, an isopod called *Excirolana linguifrons*. Territories are mainly defended in areas of intermediate prey density. At very low densities there are not enough prey to make defence worthwhile and at very high densities there are so many sanderlings trying to feed that defence would not be feasible because of high intruder pressure. In the area where birds defend territories there is an inverse correlation between territory size and food density. From Myers *et al.* (1979).

Ostriches scan at random

The precise way in which vigilance changes with flock size depends on how individuals in the group spend their time. In ostrich flocks, for example, Brian Bertram (1980) found that each individual spends a smaller proportion of its time scanning than when alone but that the overall vigilance of the group (proportion of time with at least one bird scanning) increases slightly with group size (Fig. 6.3). Therefore each bird in the flock has more time to feed and enjoys greater awareness of approaching lions (a potential predator of ostriches). The increase in vigilance with group size is as predicted if each bird raises its head independently of the others. The ostriches also raise their heads at random time intervals which makes it impossible for a stalking lion to predict how much time it has to creep forward undetected between look-ups by its victim. Any predictable pattern of looking could be exploited by the lion in its tactics of approach.

In scanning groups it may pay to cheat . . .

The problem of how individuals in a group scan is complicated by the fact that in a large group, where overall vigilance is at the maximum value of 100 per cent, it would pay an individual to

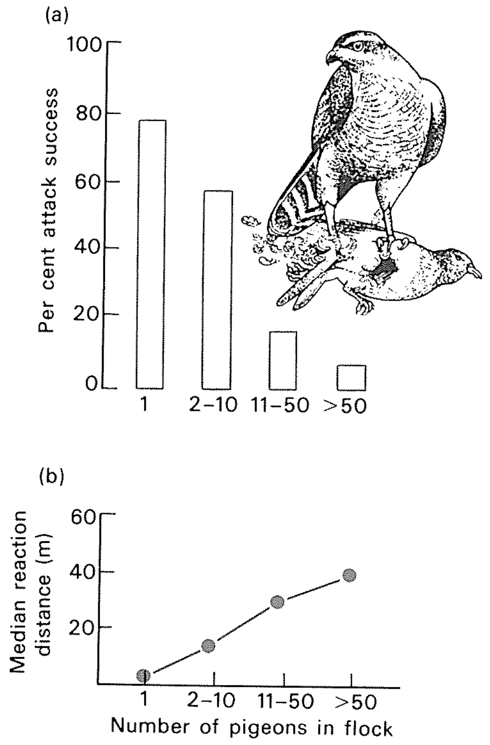

Fig. 6.2 (a) Goshawks (*Accipiter gentilis*) are less successful when they attack larger flocks of wood pigeons (*Columba palumbus*). (b) This is largely because bigger flocks take flight at greater distances from the hawk. The experiments involved releasing a trained hawk from a standard distance. From Kenward (1978).

'cheat' and spend all its time with its head down feeding. The cheater loses nothing in terms of vigilance because others are busy scanning and it gains extra time to feed. It is not known how this kind of cheating is prevented from evolving, but one suggestion is the following. Although the 'innocent' strategy of scanning regularly regardless of what others do is susceptible to cheating, a flock made up of more canny individuals, which do not scan unless they have seen their neighbours doing the same thing, might be resistant to cheaters (Pulliam *et al.* 1982). The general point is that even when there is an overall benefit of being in a group, each individual will be expected to try to get more benefit than the others. In groups of Thompson's gazelle, the individual that happens to be scanning when a predator approaches is more likely to escape (Fitzgibbon 1989). Here there is a direct benefit to the scanning individual, so no selection for cheating.

. . . unless the scanning individual gets a higher pay-off

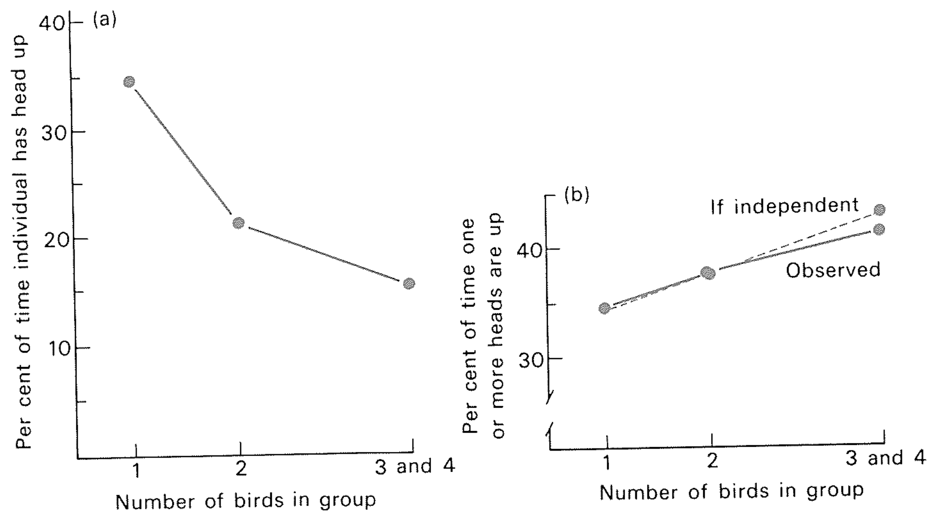

Fig. 6.3 Vigilance in groups. (a) An ostrich (*Struthio camelus*) spends a smaller proportion of its time scanning for predators when it is in a group. (b) The overall vigilance of the group increases slightly with group size (solid line), as predicted if each individual looks up independently of the others (broken line). From Bertram (1980).

DILUTION AND COVER

The dilution effect may explain . . .

Although there is only a slight increase in vigilance with increasing group size in ostriches, the chances that any one individual will be eaten during an attack by lions decreases rapidly with group size, because the lions can kill only one ostrich per successful attack. By living in a group the ostrich dilutes the impact of a successful attack because there is a good chance that another bird will be the victim. To some extent this dilution effect may be offset by the increased number of attacks on larger and more conspicuous groups, but usually the net effect probably favours living in a group, as the following hypothetical example illustrates. An individual antelope in a herd of a hundred has (all things being equal) only a one in a hundred chance of being the victim in a single attack and the herd is not likely to attract more than a hundred times as many attacks as a solitary antelope (see also Fig. 6.4). In fact if the herd is more vigilant it may pay the predator to concentrate its attacks on small groups and solitary individuals.

. . . communal roosts of butterflies . . .

One study in which the survival rate of individuals in different sized groups was measured showed an overall benefit of group living from dilution. The monarch butterfly (*Danaus plexippus*) migrates from North America to spend the winter in warmer

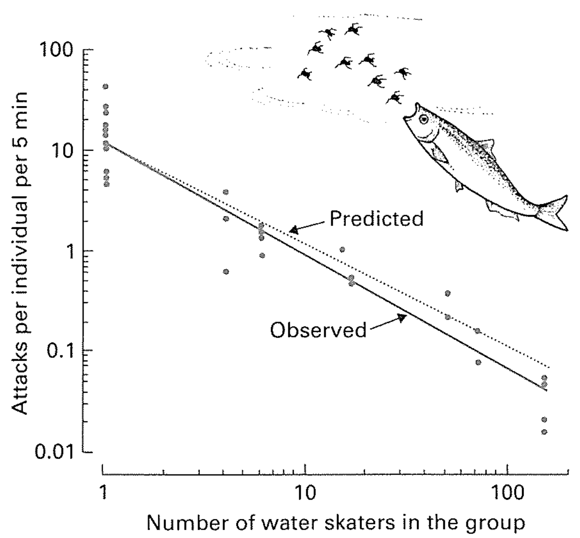

Fig. 6.4 An example of the dilution effect. The prey are insects called water skaters (*Halobates robustus*) that sit on the water surface; their predators are small fish (*Sardinops sagax*). The fish snap the insects from below, so there is little possibility that vigilance increases with group size. The attack rate by the fish was similar for groups of different sizes, so the attack rate per individual varies only because of dilution. The 'predicted' line is what would be expected if the decline in attack rate with group size is entirely caused by dilution; this line is very close to the observed. From Foster and Treherne (1981).

places such as Mexico. They assemble into enormous communal roosts in which the trees over an area of up to 3.0 ha may be clothed in resting butterflies. The monarch is not a very palatable butterfly, but some birds attack them in the winter roosts. Counts of the remains of predated butterflies showed that predation rate is inversely related to colony size, so the advantage of dilution seems to outweigh any disadvantage of greater conspicuousness in a large roost (Calvert *et al.* 1979).

. . . stealing young . . .

The dilution effect is probably a very widespread advantage of being in a group and it might explain the strange behaviour of birds such as ostriches and goosanders when they have young. When two females meet, each appears to try and steal the other's young and incorporate them into its own brood. Usually caring for someone else's young doesn't pay, but if predation pressure is severe it might, because of dilution. A more concrete example of the dilution effect comes from a study of semi-wild horses in the Carmargue, a marshy delta in the south of France. In the summer months the horses are plagued by biting tabanid flies and during this period they are more likely to cluster together in large groups.

. . . herding in horses . . .

Measurements of the number of flies per horse in large and small

groups showed that horses in a large group are less likely to be attacked. An experiment in which horses were transferred from large to small groups and vice versa confirmed that living in a group gives protection by the dilution effect (Duncan & Vigne 1979).

. . . and cicada cycles

In some animals dilution is achieved by synchrony in time as well as in space, and this might explain the remarkable 13- and 17-year life cycles of certain species of cicada. These insects live as nymphs underground and the adults emerge after 13 or 17 years depending on the species and location. In the 17-year cicada studied by Dybas and Lloyd (1974) millions of adults (of three species) emerge in synchrony over a wide area, effectively 'flooding the market' so that the chances of any one individual falling victim to a predator is reduced. Lloyd and Dybas (1966) and others have speculated on why the cycle should be 13 or 17 years long and not, for example, 15 or 18. The advantage of a very long dormant stage between emergence periods is that it forces specialist predators and parasites out of business. When there are no cicadas around for 13 or 17 years the predators have either to die or to switch to other prey or to become dormant themselves. The very long cycle could have evolved as a result of an 'evolutionary race' (Chapter 4) in which both cicadas and their predators gradually extended their life cycles until the cicadas eventually 'won'. The significance of the 13- and 17-year periods is that these are prime numbers which means that a predator could not regularly fall into synchrony with the cicadas if it had a short life cycle of which the cicada cycle is a multiple. If, for example, cicadas had a 15-year cycle, predators with 3- or 5-year life cycles would fall into step with their prey every fifth or third generation.

This idea remains an interesting speculation, but synchrony is certainly an advantage. Field evidence shows that cicadas emerging at the peak of the cycle have a lower chance of succumbing to predators than those emerging early or late (Simon 1979). Selection therefore acts to maintain synchrony once it is established.

Individuals in the middle of a group may be safer than those at the edge

Just as a cicada in the middle of the emergence period is safer than one at either end, individuals in the middle of a flock, school or herd may enjoy greater security than those at the edge. If the predators pick off victims from the edge, each member of the group should jockey for a central position and, in effect, seek cover behind the others (Hamilton 1971). This may explain why starling flocks, for example, bunch together in a tight group when a predator approaches. Why should predators attack the edge of the group? The old trick of throwing three tennis balls to a friend at the same time shows how difficult it is to track one of

Confusion effect

a number of rapidly moving objects in the visual field for long enough to catch one. There is some evidence that predators suffer from the same type of confusion when attacking a dense group of prey (Neill & Cullen 1974) and this may provide an explanation of why attacks should be directed at the edge of a group.

GROUP DEFENCE

Prey animals are often not just passive victims and by living in a group they may be able to defend themselves against the unwelcome attentions of a predator. In colonies of black-headed gulls nesting pairs will mob a crow when it flies near their nest and in the centre of a dense colony many gulls mob the crow at the same time because it is close to many nests. The effect of this is to reduce the success of the crows in hunting for gulls' eggs (Kruuk 1964) (see also Fig. 6.5a).

COSTS OF BEING IN A GROUP

Communal mobbing in fieldfares

As we mentioned earlier, one of the costs of group living might be increased conspicuousness. This cost was studied experimentally by Malte Andersson (Andersson & Wicklund 1978) using artificial nests of the fieldfare, a thrush-like bird which breeds colonially in Scandinavian boreal forests. The bulky nests are quite conspicuous and a colony of artificial nests attracted more predators than did solitary nests. However, fieldfares vigorously mob and defecate on crows and other predators, and Andersson and Wicklund found that artificial nests placed near a colony of fieldfares survived better than those placed near solitary fieldfare nests. They concluded therefore that the benefit of group mobbing by members of a colony more than offsets the disadvantage of being conspicuous. This is supported by Volker Haas's (1985) observation that nesting success is higher for colonial than for solitary fieldfares.

Living in groups and getting food

FINDING GOOD SITES

The comparative studies described in Chapter 2 revealed that species which feed on large ephemeral clumps of food such as seeds or fruits often live in groups. For these animals, the limiting stage in feeding is the problem of finding a good site: once the patch has been found there is usually plenty of food, at least for a