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Selfish individuals or group advantage?

We now return to our theme of studying the adaptive significance of behaviour, how it contributes to an individual's chances of survival and its reproductive success. We interpreted the behaviour of the lions in relation to individual advantage, reflecting Darwin's emphasis on evolution as a struggle between individuals to out-compete others in the population. Many traits evolve because of their advantage to the individual even though they are disadvantageous to others in the population. For example, it's not to the species' advantage to have a cub killed when a new male takes over a lion pride. It's not to the lionesses' advantage either! However, she is smaller than the male and there is probably not much that she can do about it. Infanticide has evolved simply because of its advantage to the male that practises it.

A few years ago, however, many people thought that animals behaved for the good of the group, or of the species. It was common to read (and sometimes still is) explanations like, 'lions rarely fight to the death because if they did so, this would endanger survival of the species' or, 'salmon migrate thousands of miles from the open ocean into a small stream where they spawn and

Behaviour of advantage to individuals may be disadvantageous to the group

die, killing themselves with exhaustion to ensure survival of the species'.

Because 'group thinking' is so easy to adopt, it is worth going into a little detail to examine why it is the wrong way to frame evolutionary arguments.

The main proponent of the idea that animals behave for the good of the group is V.C. Wynne-Edwards (1962, 1986). He suggested that if a population over-exploited its food resources it would go extinct and so adaptations have evolved to ensure that each group or species controls its rate of consumption. Wynne-Edwards proposed that individuals restrict their birth rate to prevent over-population, by producing fewer young, not breeding every year, delaying the onset of breeding, and so on. This is an attractive idea because it is what humans ought to do to control their own populations. However there are two reasons for thinking that it is unlikely to work for animal populations.

THEORETICAL OBJECTIONS

Imagine a species of bird in which each pair lays 2 eggs and there is no over-exploitation of the food resources. Suppose the tendency to lay 2 eggs is inherited. Now consider a mutant which lays 6 eggs. Since the population is not over-exploiting its food supplies, there will be plenty of food for the young to survive and the 6-egg genotype will become more common very rapidly.

Will the 6-egg type be replaced by birds that lay 7 eggs? The answer is yes, as long as individuals laying more eggs produce more surviving young. Eventually a point will be reached where the brood is so large that the parents cannot look after it as efficiently as a smaller one. The clutch size we would expect to see in nature will be the one that results in the most surviving young because natural selection will favour individuals that do the best. A system of voluntary birth control for the good of the group will not evolve because it is unstable; there is nothing to stop individuals behaving in their own selfish interests.

Group selection

Wynne-Edwards realized this and so proposed the idea of 'group selection' to explain the evolution of behaviour that was for the good of the group. He suggested that groups consisting of selfish individuals died out because they over-exploited their food resources. Groups that had individuals who restricted their birth rate did not over-exploit their resources and so survived. By a process of differential survival of groups, behaviour evolved that was for the good of the group.

In theory this might just work, but groups must be selected during evolution; some groups must die out faster than others. In

practice, however, groups do not go extinct fast enough for group selection to be an important force in evolution. Individuals will nearly always die more often than groups and so individual selection will be more powerful. In addition, for group selection to work populations must be isolated. Otherwise there would be nothing to stop the migration of selfish individuals into a population of individuals all practising reproductive restraint. Once they had arrived their genotype would soon spread. In nature, groups are rarely isolated sufficiently to prevent such immigration. So group selection is usually going to be a weak force and probably rarely very important (Williams 1966; Maynard Smith 1976a).

EMPIRICAL STUDIES

Apart from these theoretical objections, there is good field evidence that individuals do not restrict their birth rate for the good of the group but in fact reproduce as fast as they can. A good example is David Lack's long-term study of the great tit (*Parus major*) in Wytham Woods, near Oxford, England (Perrins 1965; Lack 1966).

Optimal clutch size in birds

In this population the great tits nest in boxes and lay a single clutch of eggs in the spring. All the adults and young are marked individually with small numbered metal rings round their legs. The eggs of each pair are counted, the young are weighed and their survival after they leave the nest is measured by retrapping ringed birds. This intensive field study involves several people working full-time on the great tits throughout the year, and it has been going on for 40 years! Most pairs lay 8 to 9 eggs (Fig.

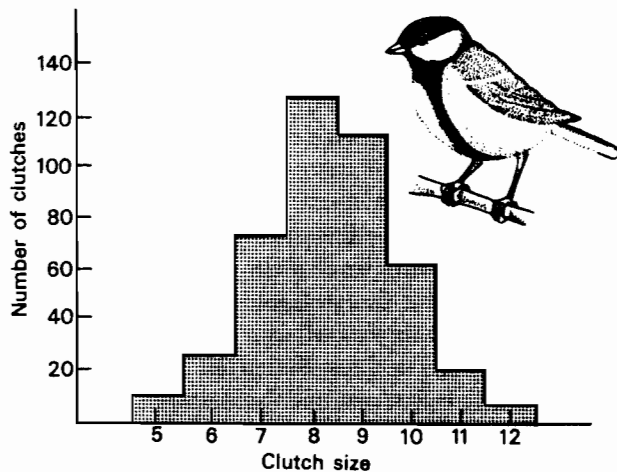


Fig. 1.3 The frequency distribution of the clutch size of great tits in Wytham Woods. Most pairs lay 8–9 eggs. From Perrins (1965).

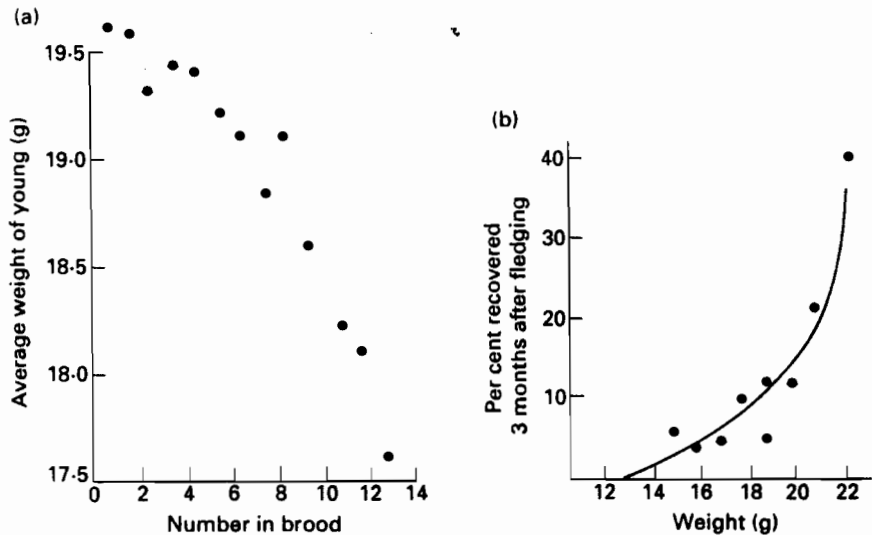


Fig. 1.4 (a) In larger broods of great tits the young weigh less at fledging because the parents cannot feed them so efficiently. (b) The weight of a nestling at fledging determines its chances of survival. Heavier chicks survive better. From Perrins (1965).

1.3). The limit is not set by an incubation constraint because when more eggs are added the pair can still incubate them successfully. However, the parents cannot feed larger broods so well. Chicks in larger broods get fed less often, are given smaller caterpillars and consequently weigh less when they leave the nest (Fig. 1.4a). It is not surprising that feeding the young produces a limit for the parents because they have to be out searching for food from dawn to dusk and may deliver over 1000 items per day to the nest at the peak of nestling growth.

The significance of nestling weight is that heavier chicks survive better (Fig. 1.4b). An over-ambitious parent will leave fewer surviving young because it cannot feed its nestlings adequately. By creating broods of different sizes experimentally it can be demonstrated that there is an optimum brood size, one that maximizes the number of surviving young from a selfish individual's point of view (Fig. 1.5). The commonest observed clutch size (Fig. 1.3) is close to the predicted optimum but slightly lower. Why is this? A possible reason is that the optimum in Fig. 1.5 is the one which maximizes the number of surviving young *per brood* whereas, at least in stable populations, we would expect natural selection to design animals to maximize their *lifetime* reproductive output. Figure 1.6 shows how the mortality costs of raising larger broods can be incorporated into our argument so as to predict the brood size which maximizes overall lifetime

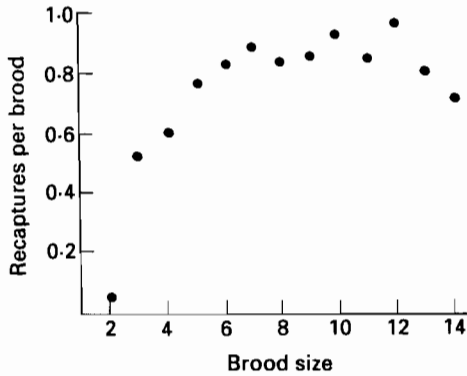


Fig. 1.5 Experimental manipulations of the number of young in a nest show that the optimal brood size for a pair of great tits is between 8 and 12 eggs. This is the brood size which maximizes the number of surviving young. From Perrins (1979).

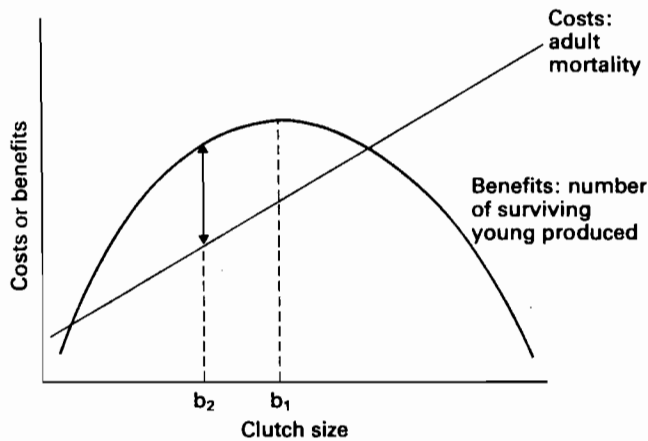


Fig. 1.6 The influence of adult mortality on the optimal clutch size. The number of young produced versus clutch size follows a curve, as in Fig. 1.5, with b_1 being the clutch size which maximizes the number of young produced per brood. Increased clutch size, however, has the cost of increased adult mortality, shown here for simplicity as a straight line. The clutch size which maximizes lifetime reproductive success is b_2 , where the distance between the benefit and cost curves is a maximum. This is less than the clutch size b_1 , which maximizes reproductive success per brood. From Charnov and Krebs (1974).

reproductive success. In general, the clutch size which maximizes lifetime breeding success will be slightly less than that which maximizes success per breeding attempt. Box 1.1 gives a more general model for the optimal trade-off between current and future reproductive effort.