

# An Introduction to Behavioural Ecology

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## Chapter 1. Natural Selection, Ecology and Behaviour

### Questions about behaviour

In this book we will explore the relationships between animal behaviour, ecology and evolution. We shall describe how animals behave under particular ecological conditions and then ask 'Why has this behaviour evolved?' For example, we shall attempt to understand why some animals are solitary while others go around in groups and why most individuals court before they copulate. Why do some birds have songs consisting of pure whistles while others produce buzzes and trills? We shall also ask some precise, quantitative questions such as why do great tits lay clutches of 8 eggs and why does the male dungfly copulate for on average 41 min?

Niko Tinbergen, one of the founders of ethology, emphasized that there are several different ways of answering the question 'Why?' in biology. These have come to be known as Tinbergen's four questions [Tinbergen 1963]. For example, if we asked why starlings, *Sturnus vulgaris*, sing in the spring, we could answer as follows.

- 1 In terms of *survival value* or *function*. Starlings sing to attract mates for breeding.
- 2 In terms of *causation*. Because increasing daylength triggers off changes in hormone levels in the body, or because of the way air flows through the syrinx and sets up membrane vibrations. These are answers about the internal and external factors which cause starlings to sing.
- 3 In terms of *development*. Starlings sing because they have learned the songs from their parents and neighbours.
- 4 In terms of *evolutionary history*. This answer would be about how song had evolved in starlings from their avian ancestors. The most primitive living birds make very simple sounds, so it is reasonable to assume that the complex songs of starlings and other song birds have evolved from simpler ancestral calls.

It is important to distinguish these various kinds of answer or otherwise time can be wasted in sterile debate. If someone said that swallows migrate south in the autumn because they are searching for richer food supplies while someone else said they migrated because of decreasing daylength, it would be pointless to argue about who was correct. Both answers may be right: the first is in terms of survival value or function and the second is in terms of causation. Factors influencing survival value are some-

Tinbergen's four  
questions

times called 'ultimate' while causal factors are referred to as 'proximate'. It is these two answers that are the most frequently muddled up and so to make the distinction clear we will discuss an example in detail.

### REPRODUCTIVE BEHAVIOUR IN LIONS

In the Serengeti National Park, Tanzania, lions (*Panthera leo*) live in prides consisting of between 3 and 12 adult females, from 1 to 6 adult males and several cubs. The group defends a territory in which it hunts for prey, especially gazelle and zebra. Within a pride all the females are related; they are sisters, mothers and daughters, cousins, and so on. All were born and reared in the pride and all stay there to breed. Females reproduce from the age of 4 to 18 years and so enjoy a long reproductive life.

For the males, life is very different. When they are 3 years old, young related males (sometimes brothers) leave their natal pride. After a couple of years as nomads they attempt to take over another pride from old and weak males. After a successful takeover they stay in the pride for 2 to 3 years before they, in turn, are driven out by new males. A male's reproductive life is therefore short.

The lion pride thus consists of a permanent group of closely related females and a smaller group of separately interrelated males present for a shorter time. We will consider three interesting observations about reproductive behaviour in a pride (Bertram 1975).

- 1 Lions may breed throughout the year but although different prides may breed at different times, within a pride all the females tend to come into oestrus at about the same time. The mechanism, or causal explanation, may be the influence of an individual's pheromones on the oestrus cycles of other females in the pride. A similar phenomenon occurs in schools, where girls living in the same dormitory may also synchronize their menstrual cycles, perhaps due to the effect of pheromones [McClintock 1971].

The function of oestrus synchrony in lionesses is that different litters in the pride are born at the same time and cubs born synchronously survive better. This is because there is communal suckling and with all the females lactating together a cub may suckle from another female if its mother is out hunting (Fig. 1.1). In addition, with synchronous births there is a greater chance that a young male will have a companion when it reaches the age at which it leaves the pride. With a companion a male is more likely to achieve a successful take-over of another pride (Bygott *et al.* 1979).

Female lions show  
synchronous oestrus

of abortion. But why are females designed in this apparently inefficient way?

One hypothesis is that it may be advantageous to the female to be receptive even at times when conception is unlikely, because this means that each copulation is devalued. For a male there is only a 1:3000 chance that a given copulation will produce a surviving cub and so it is not worth fighting with other males in the pride over a single mating opportunity. Given that males may also kill cubs that are not their own (see below), it may pay a female to mate with all the males in the pride to increase paternity uncertainty. Ideally a female may give each male a sufficient chance of being the father of her cubs that it does not pay him to kill them!

3 When a new male, or group of males, takes over a pride they sometimes kill the cubs already present (Fig. 1.1). The causal explanation for this behaviour may be the unfamiliar odour of the cubs which induces the male to destroy them. A similar effect, known as the Bruce Effect, occurs in rodents where the presence of a strange male prevents the implantation of a fertilized egg or induces abortion.

The advantage of the infanticide for the male that takes over the pride is that killing the cubs fathered by a previous male brings the female into reproductive condition again much quicker and so hastens the day that he can father his own offspring. If the cubs were left intact then the female would not come into oestrus again for 25 months. By killing the cubs she becomes ready for mating after only 9 months. Remember that a male's reproductive life in the pride is short, so any individual that practises infanticide when he takes over a pride will father more of his own offspring and therefore the tendency to commit infanticide will spread by natural selection.

The take-over of a pride by a new coalition of adult males also contributes to the reproductive synchrony of the females, because all the dependent offspring are either killed or evicted during the take-over, the females will all tend to come into oestrus again at about the same time (Packer & Pusey 1983a). Interestingly, the heightened sexual activity of the females is most marked during the first few months after a take-over. The females play an active role in soliciting copulations from several males and this appears to elicit competition between different male coalitions for the control of the pride, with the result that larger coalitions eventually become resident. This is of adaptive advantage to the female because she needs protection from male harassment of her cubs for over 2 years in order to rear her cubs successfully (3.5 months gestation plus 1.5 to 2 years with dependent young) and only

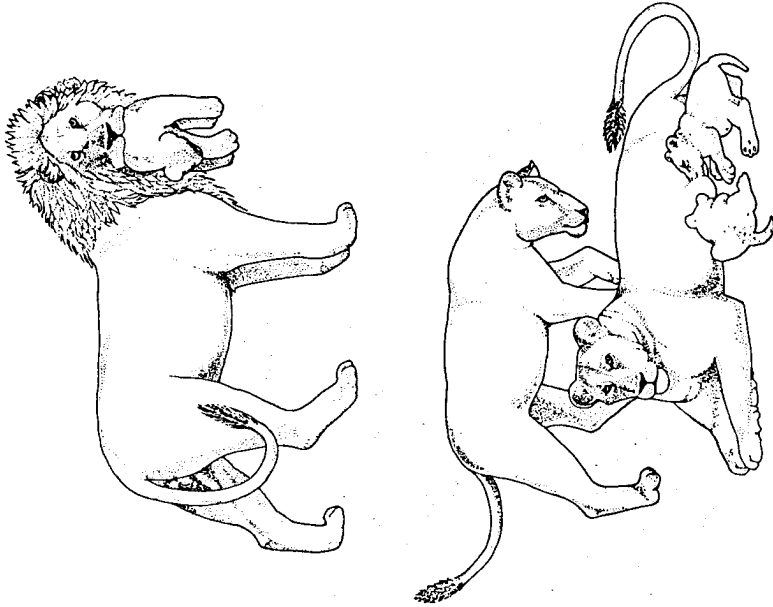


Fig. 1.1 Top: when a new male takes over a lion pride, he kills the young cubs fathered by the previous males. Bottom: a female suckles her sister's cub alongside her own.

2 A lioness comes into heat every month or so when she is not pregnant. She is on heat for 2 to 4 days during which time she copulates once every 15 min throughout the day and night. Despite this phenomenal rate of copulation the birth rate is low. Even for those cubs that are born, only 20 per cent will survive to adulthood. It can be calculated that there are 3000 copulations for each offspring that attains the adult stage.

The causal explanation for why lion matings are so unsuccessful is not the failure of the male to ejaculate but rather the high probability of ovulation failure by the female or a high rate

Males kill cubs

Causal and functional explanations of lion behaviour

and frequent copulation

adaptation could have arisen without a creator. His theory of natural selection, published in the *Origin of Species* in 1859, can be summarized as follows.

- 1 Individuals within a species differ in their morphology, physiology and behaviour (*variation*).
- 2 Some of this variation is *heritable*; on average offspring tend to resemble their parents more than other individuals in the population.
- 3 Organisms have a huge capacity for increase in numbers; they produce far more offspring than give rise to breeding individuals. This capacity is not realized because the number of individuals within a population tends to remain more or less constant over time. Therefore there must be *competition* between individuals for scarce resources such as food, mates and places to live.
- 4 As a result of this competition, some variants will leave more offspring than others. These will inherit the characteristics of their parents and so evolutionary change will take place by *natural selection*.
- 5 As a consequence of natural selection organisms will come to be *adapted* to their environment. The individuals that are selected will be those best able to find food and mates, avoid predators and so on.

When Darwin formulated his idea he had no knowledge of the mechanism of heredity. The modern statement of the theory of natural selection is in terms of genes. Although selection acts on differences in survival and reproductive success between individual organisms, or phenotypes, what changes during evolution is the relative frequency of genes.

We can restate Darwin's theory in modern genetic terms as follows.

- 1 All organisms have genes which code for protein synthesis. These proteins regulate the development of the nervous system, muscles and structure of the individual and so determine its behaviour.
- 2 Within a population many genes are present in two or more alternative forms, or alleles, which code for slightly different forms of the same protein. These will cause differences in development and so there will be variation within a population.
- 3 There will be competition between the alleles of a gene for a particular site (*locus*) on the chromosomes.
- 4 Any allele that can make more surviving copies of itself than its alternative will eventually replace the alternative form in the population. Natural selection is the differential survival of alternative alleles.

The individual can be regarded as a temporary vehicle or

Heritable variation with competition for survival and reproduction

Selection causes changes in gene frequency

large male coalitions are likely to remain in the pride for more than 2 years. High sexual activity in females may therefore incite male-male competition and so result in the best protectors taking over the pride (Packer & Pusey 1983b).

The differences between the causal and functional explanations of these three aspects of reproductive behaviour in the lions are summarized in Table 1.1.

### Natural selection

Throughout this book we will be focusing on functional questions about behaviour. Our aim is to try and understand how an animal's behaviour is adapted to the environment in which it lives. When we discuss adaptations we are referring to changes brought about during evolution by the process of natural selection. For Charles Darwin, adaptation was an obvious fact. It was obvious to him that eyes were well designed for vision, legs for running, wings for flying and so on. What he attempted to explain was how

Table 1.1 Summary of causal and functional explanations for three aspects of reproductive behaviour in lions. From Bertram (1975) and Packer and Pusey (1983a, b)

| Observation                                | Causal explanations   | Functional explanations   |
|--|---|---|
| 1 Females are synchronous in oestrus       | Chemical cues?<br>Take-overs by males                       | Better cub survival<br>Young males survive better and have greater reproductive success when they leave pride if in a group   |
| 2 High rate of copulation                  | Female infertility<br>Time of ovulation concealed           | Each copulation of less value to a male<br>Increased paternity uncertainty may protect cubs from males<br>Elicits competition between male coalitions, so females get best protectors taking over pride |
| 3 Young die when new males take over pride | Abortion (?chemical)<br>Take-over males kill or evict young | Females come into oestrus quicker<br>Male removes older cubs which would compete with his young   |

survival machine by which genes survive and are replicated (Dawkins 1976). Because selection of genes is mediated through phenotypes, the most successful genes will be those which promote most effectively an individual's survival and reproductive success (and that of relatives, see later). As a result we would therefore expect individuals to behave so as to promote gene survival.

Before we discuss how thinking about genes can help us to understand the evolution of behaviour, we should examine the evidence that gene differences can cause differences in behaviour.

### Genes and behaviour

Behavioural ecology is concerned with the evolution of adaptive behaviour in relation to ecological circumstances. Natural selection can only work on genetic differences and so for behaviour to evolve (a) there must be, or must have been in the past, behavioural alternatives in the population, (b) the differences must be, or must have been, heritable; in other words a proportion of the variation must be genetic in origin, and (c) some behavioural alternatives must confer greater reproductive success than others.

Three main methods have been used to study the ways in which genes influence behaviour.

#### (a) Use of genetic mutants

Seymour Benzer (1973) used mutagens (radiation or chemicals) to produce genetic mutations that change behaviour in the fruit fly, *Drosophila*. In one mutant, known colourfully as 'stuck', the male fails to disengage from the female after the normal 20-min period of copulation. Mutation of another gene produces 'coitus interruptus' males which disengage after only 10 min and fail to produce any offspring. Benzer was able to trace the cause of these mutations and show that they resulted from abnormalities in the sensory receptors, nervous system or muscles of the flies. Mutants which exhibit deficiencies in learning ability have also been isolated (Dudai & Quinn 1980). Normal *Drosophila* learn to selectively avoid an odour which is associated with an electric shock. Mutant 'dunce' flies do not learn to avoid the shock though they show normal behaviour in other respects and can learn visual tasks. Dunce flies are produced by an abnormality of a complex gene, at least part of which codes for the enzyme cyclic AMP phosphodiesterase, which breaks down the intracellular second messenger cAMP. Dunce flies have an abnormally high level of cAMP and, furthermore, normal flies display poor

Behavioural differences may have a genetic basis

Learning mutants in *Drosophila*

learning after being fed on phosphodiesterase inhibitors. This suggests that the enzyme is necessary for associative learning. Other learning mutants, such as 'amnesiac', which learns normally but forgets very rapidly, have also been isolated. In all cases the mutations perturb second messenger systems (Dudai 1989).

#### (b) Artificial selection experiments

Selected lines are produced by choosing as parents in each generation those individuals which show the most extreme values of some behaviour character. For example, Aubrey Manning (1961) was able to select for two different mating speeds in the fruit fly, *Drosophila melanogaster*, by selectively breeding from fast and slow maters. Such selection experiments nearly always work, showing that much of the continuous phenotypic variation seen in populations has some genetic basis. Another example is provided by male field crickets, *Gryllus integer*, which either call to attract females or silently intercept females attracted to the callers. Cade (1981) was able to select for males which called a lot and those which called only rarely, thus showing that variation in calling duration had a genetic component.

Genetic differences in cricket calling . . .

#### (c) Studying populations with genetic differences

Geographically distinct populations of a species often have a different morphology and behaviour, reflecting adaptations to differing ecological conditions. Stevan Arnold (1981) studied the garter snake, *Thamnophis elegans*, in the south-west United States. Inland populations are very aquatic and commonly feed underwater on frogs, fish and leeches. Coastal populations are terrestrial foragers and mainly eat slugs. In laboratory choice experiments it was found that wild-caught inland snakes refused to eat slugs, though the coastal ones readily accepted them. Tests with naive newborn snakes showed that 73 per cent of the coastal individuals attacked and ate slugs while only 35 per cent of the inland snakes did so. Young snakes are incubated inside their mother and so one possibility is that the mother's diet could influence the young directly. Arnold arranged matings between inland and coastal individuals and found that the offspring tended to show an intermediate incidence of slug eating. They did not tend to resemble their mother as opposed to their father and so the influence of maternal diet can be ruled out. These results suggest that differences in food preference are correlated with genetic differences, and that garter snakes in different areas have been selected to respond to different prey types.

. . . and food preferences of snakes

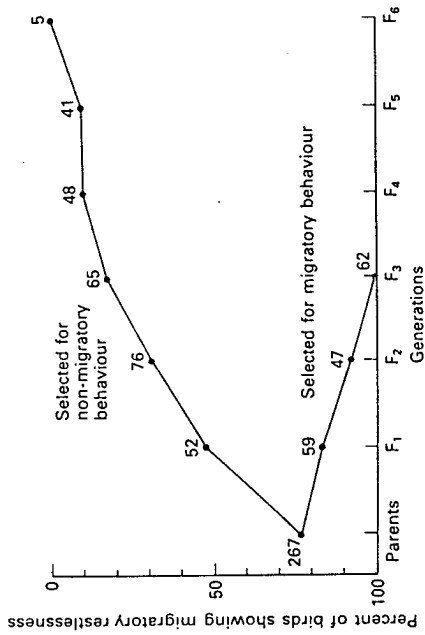


Fig. 1.2 Selection for migratory or non-migratory behaviour in blackcaps. The numbers indicate how many birds were hand-raised in each generation. Starting from a parental stock in which about 75 per cent of birds migrate, the selection experiment produced a population of non-migrators in six generations, and another line of migrators in three generations. In each generation, half the pairs were first-year birds and half were mixed first-year × older bird pairs. (Note that the vertical axis of the graph has a reversed scale.)

ecologically important trait such as migration may respond rapidly to selection.

These various examples show that genetic differences between individuals can lead to differences in behaviour (mating behaviour, learning, singing, foraging and migration). Three points need to be emphasized. First, when we talk about 'genes for' a particular structure or behaviour, we do not imply that one gene alone codes for the trait. Genes work in concert and it is likely that many genes together will influence an individual's mating preference, foraging habits and migration patterns. However, a difference in behaviour between two individuals may be due to a difference in one gene. A useful analogy is the baking of a cake. A difference in one word of a recipe may mean that the taste of the whole cake is different, but this does not mean that the one word is responsible for the entire cake (Dawkins 1978). Whenever we talk about 'genes for' certain traits this is shorthand for gene differences bringing about differences in behaviour.

Second, genes will often influence behaviour in simple ways. Gene differences can result in behavioural differences because genes code for enzymes which influence the development of the sensory, nervous and muscle systems of the animal which in turn affect its behaviour. For example, a gene could influence a

Most species of warblers are summer visitors to Europe. If individuals are kept in a cage, they show a period of 'restlessness' in the autumn which corresponds with the time at which they would migrate south to Africa for the winter. Quantitative comparisons of the nocturnal restlessness of caged experimental birds showed that the duration of the restlessness correlated well with the distance which the individuals migrated.

Peter Berthold (Berthold *et al.* 1990a,b) has carried out a series of large-scale experiments on blackcaps (*Sylvia atricapilla*) to investigate the genetic basis of both the duration of migratory restlessness and the direction of migratory orientation, measured in cages. Blackcaps are ideal for such a study because different populations show differing degrees of migratory behaviour: in southern Germany, for example, all birds migrate, and in the Cape France only a part of the population migrates, and in the Cape Verde Islands, the population is entirely sedentary. To what extent do these inter-population differences reflect genetic differences? Berthold has investigated this question by two kinds of experiment: cross-breeding of birds from different populations, and selection experiments. Both kinds of study involved breeding blackcaps in captivity and studying the migratory behaviour of offspring in cages equipped with electronic perches to record migratory restlessness.

Hybrids between parents from southern Germany (migratory) and the Cape Verde Islands (resident) had intermediate behaviour. About 40 per cent of the offspring showed migratory restlessness and the remainder did not. Furthermore, the preferred average directional heading shown by the migratory hybrid offspring was indistinguishable from that of the German parents. These results show that the difference between the two populations has a genetic basis. They suggest that more than one gene is involved (otherwise the offspring would all resemble the dominant parent) and that the effect of several genes is likely to have a threshold effect (otherwise all offspring would be intermediate between the two parents).

Berthold's selection experiments also confirm a genetic basis to differences in migratory behaviour. Among 267 hand-raised blackcaps from a population in the Rhone Valley of southern France, three-quarters were migratory and one-quarter resident, when tested in the laboratory. By selectively breeding from migratory and non-migratory parents, Berthold was able to produce strains of blackcaps that were either 100 per cent migratory (in three generations) or 100 per cent residents (in six generations) (Fig. 1.2). Not only does this experiment confirm a genetic basis to differences in migratory behaviour, but it also shows how an

Behaviour differences caused by gene differences

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.

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

moth's preference for a particular background by coding for certain visual pigments in the eye. Third, just because it can be shown that genes influence behaviour this does not imply that genes alone produce the behaviour, or even that the behaviour can be usefully divided up into genetic and environmental components. The way in which behaviour develops is the result of a complex interaction between genes and environment. Imagine, for example, that a behavioural ecologist comes across the nest of a long tailed tit (*Aegithalos caudatus*). He or she would be immediately impressed by how well the nest was adapted to the bird's way of life, the wonderful crypsis of the nest, its strength and warmth. There are three different ways in which this adaptation could develop in an individual (Bateson 1983). Individuals could all learn by trial and error how to build good nests. Alternatively they could copy another, more experienced bird. Finally, during evolution genes necessary for the expression of actions leading to the construction of good nests could have spread through the population by natural selection because individuals building the best nests would have left most young. Thus, all individuals may be able to build good nests without practice or observing others. However, even if nest building required learning for its proper development, genetic differences in learning ability may still be involved in its evolution.

#### 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

Group selection

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).

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.

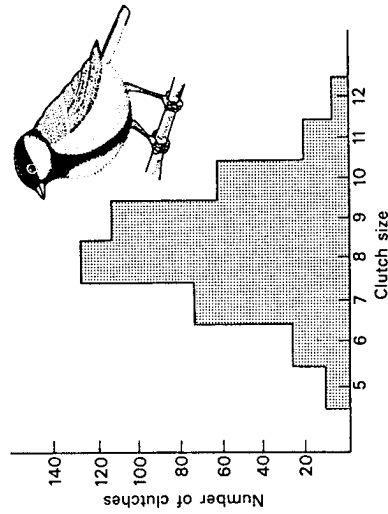


Fig. 1.3 The frequency distribution of the clutch size of great tits in Wytham Woods. Most pairs lay 8–9 eggs. From Perrins (1965).

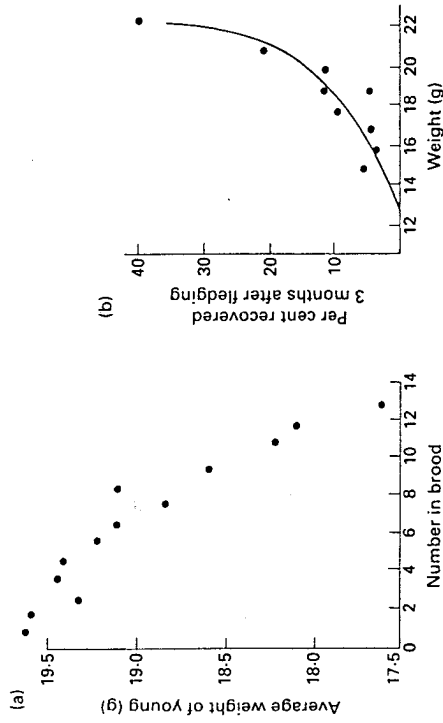


Fig. 1.4 (a) In larger broods of great tits the young weigh less at fledging because the parents cannot feed them so efficiently. (b) The weight of a nestling at fledging determines its chances of survival. Heavier chicks survive better. From Perrins (1965).

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.

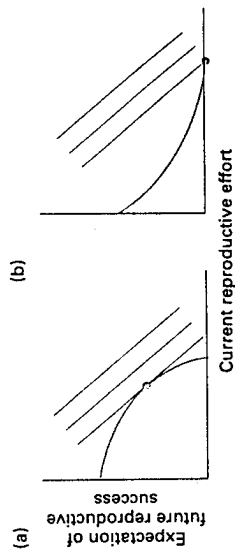
The significance of nestling weight is that heavier chicks survive better (Fig. 1.4b). An over-ambitious parent will leave fewer surviving young because it cannot feed its nestlings adequately. By creating broods of different sizes experimentally it can be demonstrated that there is an optimum brood 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

Survival versus reproduction



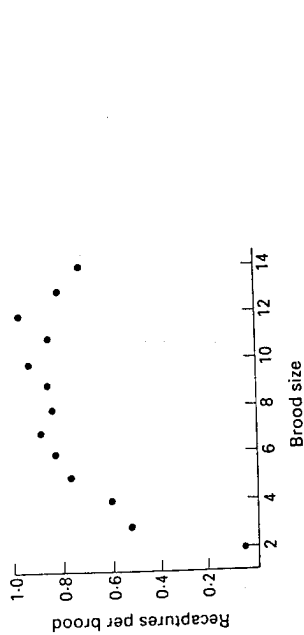
**Box 1.1** *The optimal trade-off between survival and reproductive effort.* From *Pianka and Parker (1975)* and *Bell (1980)*.

The more effort an individual puts into reproduction, the lower its chances of survival and so the lower its expectation of future reproductive success. Reproductive costs include allocation of resources to reproduction which would otherwise have been spent on own growth and survival and the increased risks entailed in reproduction, such as exposure to predators. The optimal life history depends on the shape of the curve relating profits in terms of present offspring to costs in terms of future offspring.

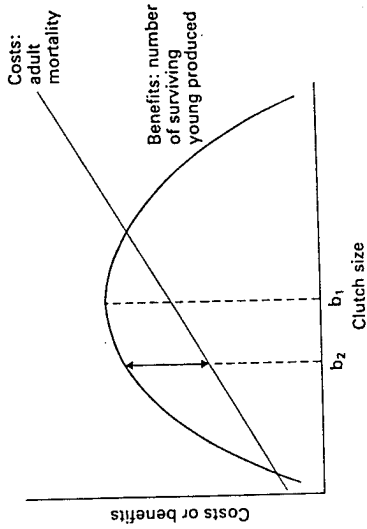


The families of straight lines represent fitness isoclines, i.e. equal lifetime production of offspring. In a stable population, present and future offspring will be of equal value and these lines will have slopes of  $-1$ . In an expanding population, current offspring are worth more than future offspring [current offspring gain a greater contribution to the gene pool] and the slopes are steeper. In a declining population future offspring are worth more and slopes will be less than  $-1$ .

The point of intersection of the curves relating the trade-off between current and future reproductive success, with the fitness isocline furthest from the origin gives the optimal reproductive tactic (indicated by solid dot). When the trade-off curve is convex [a], fitness is maximized by allocating part of the resources to current reproduction and part to survival [i.e. iteroparity, or repeated breeding]. When the curve is concave [b], it is best to allocate all resources to current reproduction even at the expense of own survival (semelparity, or 'big bang' suicidal reproduction). If maximal future reproductive success is greater than maximal current reproductive success in case [b], then the optimal tactic is to not breed and save all resources for the future.



**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.

Table 1.2 A comparison of the clutch size of European passerine birds grouped into two ecological categories. Hole nesting species have larger clutches. From Lack (1968)

| Nest type | Predation | Average clutch size | Average length of nestling period (days) |
|-----------|-----------|---------------------|--|
| Holes     | Low       | 6.9                 | 17                                       |
| Open      | High      | 5.1                 | 13                                       |

in clutch size occurred because there was a range of territory quality and each pair raised a brood size appropriate for its own particular territory. Experiments have shown similar individual optimization of clutch size in great tits (Pettifor *et al.* 1988) and collared flycatchers (Gustafsson & Sutherland 1988).

One of the main themes of this book is that different life history strategies will be favoured in different ecological circumstances. For example, continuing our discussion of clutch size, if the European passerine bird species are grouped into two ecological categories, namely those that nest in holes and those that build open nests, it is found that the hole nesters lay larger clutches (Table 1.2). The same relationship occurs in ducks where open nesting species again have smaller clutches than hole nesters (Lack 1968). In holes the young are relatively safe from predators but in the open there is a premium for getting the young out of the vulnerable nest as soon as possible. The same quantity of food could be used to rear a small brood quickly or a larger brood more slowly. In open nesting species the higher risks of predation have apparently selected for a smaller clutch size and rapid nestling growth.

**Behaviour, ecology and evolution**

We are now in a position to summarize the main principles which underlie the arguments in this book. First, during evolution natural selection will favour individuals who adopt life history strategies which maximize their gene contribution to future generations. Second, the way in which adult survival and reproductive effort are best traded-off in a life history will depend on ecology, the physical environment an individual lives in, its competitors, food, predators, and so on. Third, because an individual's success at surviving and reproducing depends critically on its behaviour, selection will tend to design animals as efficient foragers, efficient predator avoiders, efficient copulators, efficient parents, and so on. What will be 'optimal' will depend on the

Hole-nesting species lay larger clutches

As yet there is no evidence for increased mortality costs from raising larger broods in the great tit. When Pettifor *et al.* (1988) manipulated brood size by adding or removing 3-4 young soon after hatching, parents raising enlarged broods survived just as well to the next season as those which raised their own natural brood size or a decreased brood. Whether this means that there is no cost of reproduction, or that the cost is hard to measure, needs further work. In blue tits (*Parus caeruleus*) similar brood manipulations did reveal significant survival costs in some years but not in others, so longer-term studies are needed for a proper evaluation (Nur 1988).

Our conclusion is that reproductive rate is close to that which maximizes individual success. Thus clutch size is optimal from the selfish individual's point of view. Of course, the exact clutch size may vary a little from year to year and during the season depending on food supplies, so individuals do show some variation. However the variations are in relation to their own selfish optima, not for the good of the group. A good example of this is provided by Goran Högstedt's study (1980) of magpies, *Pica pica*, breeding in southern Sweden. Observed clutch sizes varied from 5 to 8 depending on feeding conditions in different territories. Our hypothesis would be that some females laid only 5 eggs because this was the maximum number of young they could raise efficiently on their particular territories. Högstedt manipulated clutch sizes experimentally and found that pairs that had produced large clutches did best with large broods, while those which had laid small clutches did best with smaller broods (Fig. 1.7). Variation

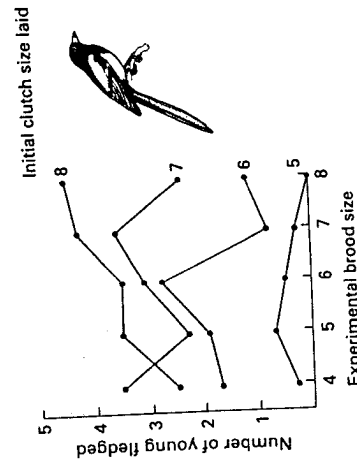


Fig. 1.7 Experiments on clutch size in magpies. Pairs which had initially laid 5, 6, 7 or 8 eggs were given experimentally reduced or enlarged broods. Pairs which had naturally laid large clutches did better with large broods and vice versa. From Högstedt (1980).

Individuals may have different optima

Montgomerie and Weatherhead (1988) discuss how the trade-off between current and future reproductive success influences nest defence by parent birds.

#### Topics for discussion

- 1 How would you test the causal and functional explanations for lion behaviour in Table 1.1.1?
- 2 Under what conditions would the trade-off between present and future reproduction look like (a) or (b) in Box 1.1.1?
- 3 What do you understand by the term 'optimal clutch size'?

behavioural alternatives available which will depend on various constraints imposed by phylogeny, physiology and ecology.

Behavioural ecology, therefore, is a meeting point for behaviour, ecology and evolution. We can think of ecology as setting the stage on which animals must perform their behaviour, and evolution as a process which selects individuals whose behaviour results in greatest success in the struggle to contribute genes to the population's gene pool. The aims of the subject are to understand why different species behave in different ways and why, within a species, there may also be individual differences in behaviour. To tackle these problems we have to learn about a species' ecology and also about how individuals in a population compete for scarce resources, such as food, mates and territories.

#### Summary

Behavioural ecology is concerned with functional questions about behaviour, namely how a particular behaviour pattern contributes to an animal's chances of survival and its reproductive success. Experiments show that differences in behaviour can result from differences in genes. Natural selection will favour genes which best promote an individual's chances of passing those genes on to future generations. Individuals are expected to behave in their own selfish interests and not for the good of the species or group. Ecological conditions will determine which behaviour patterns are favoured during evolution.

#### Further reading

The books by G.C. Williams (1966) and Richard Dawkins (1976, 1982) are excellent discussions of behaviour and evolution. Williams emphasizes the evolution of individual selfishness as opposed to behaviour for the good of the group. Dawkins champions the view that we should think in terms of genes rather than individuals in order to understand the evolution of behaviour.

Partridge (1983) and Bateson (1983) discuss how genes influence behaviour. Southwood (1981) and Lessells (1991) show how different life histories are favoured under different ecological conditions.

In this chapter we have discussed optimal clutch size from the parent's point of view. In fact there will be conflicts of interest between the male and female [see Chapter 9], between parents and offspring (Trivers 1974), and between members of the brood. Mock (1984, 1985) shows how chicks within a brood may kill their siblings when competing for food brought by the parents.