CHAPTER 1

Natural Selection, Ecology and Behaviour

Photo © Craig Packer

Watching and wondering

Imagine you are watching a bird searching in the grass for food (Fig. 1.1). At first your curiosity may be satisfied simply by knowing what species it is, in this case a starling *Sturnus vulgaris*. You then watch more closely; the starling walks along and pauses every now and then to probe into the ground. Sometimes it finds a prey item, such as a beetle larva, and eventually, when it has collected several prey items, it flies back to the nest to feed its hungry brood.

For students of behavioural ecology, a whole host of questions comes to mind as this behaviour is observed. The first set of questions concerns how the bird feeds. Why has it chosen this particular place to forage? Why is it alone rather than in a flock? Does it collect every item of food it encounters or is it selective for prey type or size? What influences its decision to stop collecting and fly back to feed its chicks?

Another set of questions emerges when we follow the starling back to its nest. Why has it chosen this site? Why this number of chicks in the nest? How do the two adults decide on how much food each should bring? Are these two adults the mother and father of all the chicks? Why are the chicks begging so noisily and jostling to be fed? Surely this would attract predators to the nest. If we could follow our starlings over a longer period, we may then begin to ask about what determines how much effort the adults put into reproduction versus their own maintenance, about the factors influencing the timing of their seasonal activities, their choice of mate, the dispersal of their offspring and so on.

Asking questions

Behavioural ecology provides a framework for answering these kinds of questions. In this chapter we will show how it combines thinking about behaviour, ecology (the 'stage' on which individuals play their behavioural strategies) and evolution

(how behaviour evolves by natural selection). But first, we need to be clear about exactly what we mean when we ask the question 'why?'

Tinbergen's four 'why' questions

Niko Tinbergen (1963), one of the founders of scientific studies of animal behaviour in the wild, emphasized that there are four different ways of answering 'why' questions about behaviour. For example, if we asked why male starlings sing in the spring, we could answer as follows:

(1) In terms of *causation*. Starlings sing because the increasing length of day triggers changes in their hormones, or because of the way air flows through the vocal apparatus and sets up membrane vibrations. These are answers about the mechanisms that cause starlings to sing, including sensory and nervous systems, hormonal mechanisms and skeletal–muscular control.

(2) In terms of *development or ontogeny*. For example, starlings sing because they have learned the songs from their parents and neighbours, and have a genetic disposition to learn the song of their own species. This answer is concerned with genetic and developmental mechanisms.

(3) In terms of *adaptive advantage or function*. Starlings sing to attract mates for breeding, and so singing increases the reproductive success of males.

(4) In terms of *evolutionary history or phylogeny*. 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.

Proximate versus ultimate explanations   Causal and developmental factors are referred to as *proximate* because they explain how a given individual comes to behave in a particular way during its lifetime. Factors influencing adaptive advantage and evolution are called *ultimate* because they explain why and how the individual has evolved the behaviour. To make the distinction clearer, an example is discussed in detail.

Reproductive behaviour in lions

In the Serengeti National Park, Tanzania, lions (*Panthera leo*) live in prides consisting of between three and twelve adult females, from one to six adult males and several cubs (Fig. 1.2a). 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 four to eighteen years and so enjoy a long reproductive life.

For the males, life is very different. When they are three 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

Fig. 1.1   A foraging starling. Photo © iStockphoto.com/ Dmitry Maslov

(a)

Fig. 1.2 (a) A lion pride. (i) The females are returning to the middle of their territory after chasing away a neighbouring pride. (ii) Females and cub. (iii) Males patrolling the territory and (iv) relaxing. (v) Male with cub. Photos © Craig Packer (b) Infanticide: a male that has just taken over ownership of a pride, with a cub in his jaws that he has killed. Photo © Tim Caro

they stay in the pride for two to three 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. Brian Bertram (1975) considered two interesting observations about reproductive behaviour in a pride.

Female lions show synchronous oestrus

(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, is likely to be the influence of pheromones on oestrus cycles (Stern & McClintock, 1998). But why are lionesses designed to respond in this way? One adaptive advantage of oestrus synchrony 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. In addition, with synchronous births there is a greater chance that a young male will have a similar-aged 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; Packer *et al.* 1991).

Males kill cubs after take-over

(2) When a new male, or group of males, takes over a pride they sometimes kill the cubs already present (Fig. 1.2b). The causal explanation is not known but it may be the unfamiliar odour of the cubs that induces the male to attack them. But, whatever the mechanism, why are male lions designed to respond in this way?

The benefit of 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 more quickly. This 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 the male makes her ready for mating after only nine 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, 1983b). Interestingly, the sexual activity of the females is most intense 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 two years in order to rear her cubs successfully (3.5 months gestation plus 1.5–2 years with dependent young) and only large male coalitions are likely to remain in the pride for more than two years. High sexual activity in females at around the time of take-overs may therefore incite male–male competition and so result in the best protectors taking over the pride (Packer and Pusey, 1983a).

Observation	Causal explanations	Functional explanations
1 Females are synchronous in oestrus	Chemical cues? Take-overs by males	Better cub survival Young males survive better and have greater reproductive success when they leave pride if in a group
2 Young die when new males take over pride	Abortion Take-over males kill or evict young	Females come into oestrus more quickly Male removes older cubs which would compete with his young

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

The differences between the causal and functional explanations of these two aspects of reproductive behaviour in the lions are summarized in Table 1.1. The key point is that causal explanations are concerned with mechanisms, while functional explanations are concerned with why these particular mechanisms (rather than others) have been favoured by natural selection.

Causal and functional explanations of lion behaviour

Natural selection

The aim of behavioural ecology 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 adaptation could have arisen without a creator or, put another way, how you could get the appearance of design without a designer. His theory of natural selection, published in the *Origin of Species* (Darwin, 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.

Heritable variation with competition for survival and reproduction

(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 be those that are best at competing for the scarce resources. Their offspring

will inherit the characteristics of their successful parents and so, through *natural selection* over the generations, organisms will come to be *adapted* to their environment. The individuals that are selected, naturally, will be those best able to find food and mates, avoid predators and so on.

(5) If the environment changes, then new variants may do best and so natural selection can lead to *evolutionary change*.

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 proteins. These proteins regulate the development of the nervous system, muscles and structure of the individual, and so influence its behaviour.

(2) Within a population many genes are present in two or more forms, or alleles, which code for slightly different forms of the same protein or determine when, where and how much of the protein is expressed. These will cause differences in development and function, and so there will be variation within a population.

Selection causes changes in gene frequency

(3) Any allele that results in 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 through their effects on replication success.

The individual can be regarded as a temporary vehicle or survival machine by which genes survive and replicate (Dawkins, 1976). Because selection of genes is mediated through phenotypes, the most successful genes will usually be those that are most effective in enhancing an individual's survival and reproductive success (or that of relatives, as we shall show later in the book).

Genes and behaviour

Natural selection can only work on genetic differences, 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.

Behavioural differences may have a genetic basis

Some examples to show how *genetic differences* between individuals can lead to *differences in behaviour* are now discussed. Note the emphasis on the word *difference*. 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 many genes together will influence an individual's mating preference, foraging, migration and so on. However, a *difference* in behaviour between two individuals may be due to a *difference* in one (or more) genes. A useful analogy is the baking of a cake. A difference in one word of a recipe (one versus two spoonfuls) 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.

Three other important points should be borne in mind when reading these examples. Firstly, the molecular path linking genes and behaviour is complicated (transcription, translation, influence on sensory systems, neural activity, brain metabolism and so on). Secondly, the arrow linking genes and behaviour goes in both directions (Robinson *et al.*, 2008). Not only do genes influence behaviour, through effects on brain development and physiology, but behaviour can also influence gene expression. Thirdly, just because it can be shown that genes influence behaviour does not imply that genes alone produce the behaviour. Behavioural development is an outcome of a complex interaction between genes and environment. The examples now discussed help to make these general points clearer.

Drosophila and honeybees: foraging, learning and singing

Larvae of the fruit fly *Drosophila melanogaster* feed in one of two distinct ways. 'Rovers' wander around in search of food while 'sitters' tend to remain in one small area to feed. These differences persist into the adult stage, with rover flies also searching more widely when foraging. In the absence of food, rovers and sitters (larvae or adults) do not differ in general activity. This difference in foraging strategies is caused by a difference in just one gene (the *foraging* gene, *for*) which codes for an enzyme which is rather snappily called cyclic guanosine monophosphate (cGMP) dependent protein kinase (PKG). This enzyme is produced in the brain and influences behaviour. Flies with the 'rover' allele (*for^R*) show higher PKG activity than those homozygous for the 'sitter' allele (*for^s*). When the *for^R* allele is inserted into the genome of sitter larvae, they become rovers (Osborne *et al.*, 1997).

Rovers and sitters in *Drosophila*

Individuals with the *for^R* allele also have better short-term memory for olfactory stimuli, while those with the *for^s* allele perform better at long-term memory tasks involving odour cues. These differences may be coadapted with the differences in foraging behaviour: rovers may benefit from fast learning as they move between food patches, while sitters, with a sedentary feeding style, may benefit from long-term memory (Mery *et al.*, 2007).

In one orchard population in Toronto, 70% of larvae was rovers while 30% was sitters. Why do the two feeding types persist? Laboratory experiments reveal that rovers do best under patchy food and high larval densities (rovers are better at finding new food patches) while sitters do best with more uniformly distributed food and at low larval density (when roving is unnecessary as local food is abundant; Sokolowski *et al.*, 1997). Therefore, each morph does best under different ecological conditions. However, a further factor is involved in maintaining the polymorphism. When food is scarce, competition is most intense between individuals of the same morph: sitters compete most with sitters within local food patches, while rovers compete most with other rovers over the discovery of new food patches. This leads to the situation where the rarer type has an advantage, which is termed negative frequency-dependent selection; in a population of rovers a sitter does especially well, while in a population of sitters a rover

does especially well. Because each type does better when rare, this will tend to maintain the behavioural polymorphism (Fitzpatrick *et al.*, 2007). This topic is discussed further in Chapter 5.

Gene expression and behaviour changes with age in honeybees

The same *foraging* gene, *for*, regulates age changes in foraging worker honeybees, *Apis mellifera*. When they are young, adult worker bees perform various tasks inside the hive, such as storing food and caring for the brood. Then, when they are about three weeks old, they begin to go off on long foraging flights to collect pollen and nectar for the colony. This marked change from 'sitting at home' to 'roving for food' involves changes in the expression of *for*, with foragers having increased production of the enzyme PKG. When young workers were induced to switch to foraging earlier (one week of age) by removal of older workers, these precocious foragers also had increased *for* expression. Therefore, expression of *for* was related to social information (presence or absence of older workers), which then influenced foraging activities; it was not just a response to age. Finally, experimental elevation of PKG activity in young workers also led to a switch to foraging behaviour (Ben-Shahar *et al.*, 2002).

Thus, in *Drosophila* different individual foraging behaviours are caused by differences in alleles of the *for* gene, while in honeybees the switch in behaviour within individuals is caused by changes in *for* gene expression.

Drosophila courtship song

Single gene differences can also cause differences in *Drosophila* courtship song. Males produce a courtship song by vibrating their wings and the temporal pattern of the song varies between species. Breeding experiments and molecular genetic analysis reveal that these differences in song structure are caused by differences in the *period* gene. Transfer of a small piece of the *period* gene from *D. simulans* to *D. melanogaster* causes *melanogaster* males to produce the *simulans* song rather than *melanogaster* song (Wheeler *et al.*, 1991).

MC1R: mate choice and camouflage

A gene influencing melanin

The lightness or darkness of skin, hair or feathers depends primarily on the amount of a pigment, melanin, produced by specialised skin cells (melanocytes). The MC1R gene (melanocortin-1 receptor) encodes a receptor that is expressed in melanocytes. The activity of this receptor regulates the amount and type of melanin synthesis. Point mutations in this gene are associated with colour variation in fish, reptiles, birds and mammals, so this gene has been conserved through a long evolutionary history.

In lesser snow geese (*Anser chen caerulescens*) there are two colour morphs, white and blue. Individuals that are homozygous for one variant allele at MC1R are white, while those that are heterozygous or homozygous for the other allele are blue. Curiously, there is no evidence for any selective advantage in being either white or blue. However, colour influences the choice of mate. There is assortative mating by colour (white with white, blue with blue) and young goslings imprint on their parents' colour and then favour a mate of the same colour (Mundy *et al.*, 2004).

Variation in the same gene controls colour in the rock pocket mouse (*Chaetodipus intermedius*). In the Pinacate desert of Arizona, the mouse occurs in two colour forms. Dark, melanic mice live on black lava flows while sandy-coloured mice live in sandy, desert habitat. There is selective predation by owls against mice which do not match their background (Nachman *et al.*, 2003).

Blackcaps: migratory behaviour

The cases discussed so far involve single gene differences causing marked differences in phenotype. Often, however, phenotype differences reflect the effects of many genes acting in concert. Migration behaviour provides an excellent example.

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 at the time they would migrate south to the Mediterranean or beyond to Africa. Quantitative comparisons between populations breeding at different latitudes have shown that the duration of restlessness correlates with migration distance, while the direction of fluttering in the cage correlates with migration direction. Therefore, migration behaviour can be studied experimentally in caged birds.

Peter Berthold and colleagues have investigated the genetic basis for migration distance and direction in blackcaps, *Sylvia atricapilla* (Fig. 1.3a). Populations in southern Germany are highly migratory while those in the Canary Islands are sedentary. When birds from these two populations were cross-bred in aviaries, their offspring showed intermediate migratory restlessness, suggesting genetic control (Fig. 1.3b). Selection experiments confirmed that there was a genetic basis to differences in migration behaviour. Among 267 hand-raised blackcaps from a population in the Rhone Valley of southern France, three-quarters showed migratory restlessness while one quarter did not. By selectively breeding from either migratory or non-migratory parents, lines of blackcaps were produced that were either 100% migratory (in three generations) or 100% resident (in six generations). Furthermore, among the migrant individuals migratory activity had also responded to selection (Fig. 1.3c). Not only does this experiment reveal a genetic basis to migratory behaviour, it also shows how rapidly migration may evolve.

Selection experiments for migration behaviour

Finally, and thrillingly, Berthold and coworkers have discovered an example of evolution in action. Central European populations of blackcaps traditionally winter to the southwest of their breeding grounds in the western Mediterranean (Fig. 1.3d). During the past 40 years, however, the number of blackcaps wintering in Britain and Ireland (1500km to the north of the traditional wintering grounds) has steadily increased. At first, it was assumed that these must be British breeding birds, remaining in response to milder winters. However, ringing recoveries indicated that they were breeders from central Europe with an entirely new migration habit. Blackcaps wintering in Britain were caught and kept in aviaries. When their migration behaviour was tested in cages, they exhibited a westerly autumn migration direction, shifted c70° from the traditional south-westerly route. Furthermore, their offspring inherited this new autumnal orientation (Fig. 1.3d).

A new migration habit – evolution in action

The new migration direction is probably being favoured because of milder winters and more winter food in Britain, both from garden feeders and winter fruit bushes planted in recent decades. This new population of migrants enjoys a shorter distance to winter quarters and an earlier arrival back in the central European breeding grounds in spring. This enables them to gain the best breeding territories and to produce more offspring (Bearhop *et al.*, 2005). The different arrival times on the breeding grounds also lead to assortative mating by wintering area (males wintering in Britain tend to pair with females wintering in Britain) and hence restricted gene flow, which has likely contributed to the rapid evolution of the new migration behaviour (Bearhop *et al.*, 2005).
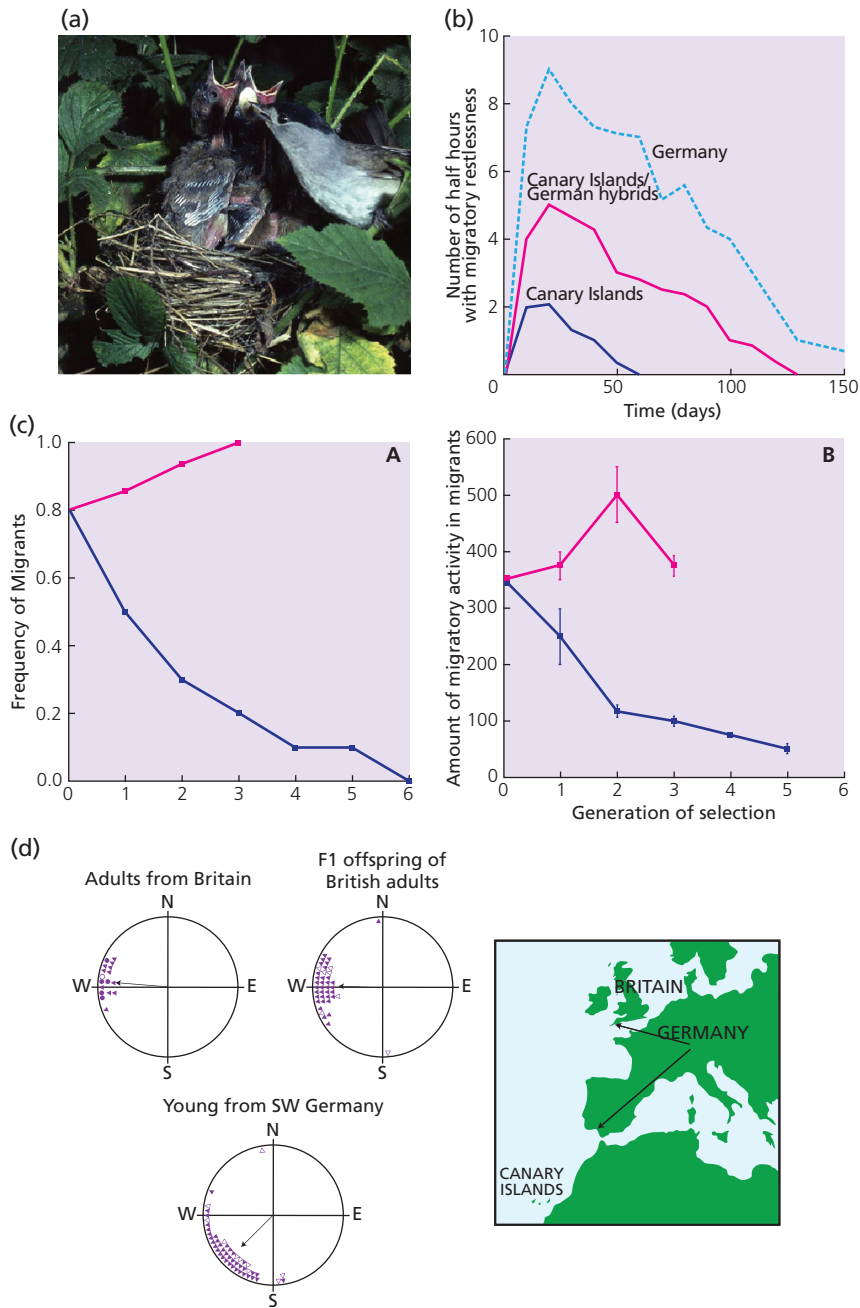
Fig. 1.3 Blackcap migration. (a) Male blackcap with nestlings. Photo © W. B. Carr (b) Migratory restlessness (measured in cages) during the time of autumn migration in blackcaps from Germany, the Canary Islands and F_1 hybrids of these two populations. From Berthold and Querner (1981). Reprinted with permission from AAAS. (c) Artificial selection in aviary populations for higher (red) and lower (blue) migratory behaviour in a partially migratory blackcap population from southern France; A: frequency of migrant individuals; B: migratory activity in migrants. From Berthold *et al*. (1990) and Pulido *et al*. (1996). (d) Traditionally, in autumn blackcaps from southern Germany migrate in a south-west direction to winter in the western Mediterranean region. During the past 40 years a new migration habit has evolved, with some blackcaps migrating west to Britain; F_1 offspring from these adults inherit the new direction. Each point in the circles to the left refer to the direction of migration of one caged individual and the arrows indicate the mean direction). From Berthold *et al*. (1992). Reprinted with permission from the Nature Publishing Group.

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 is not to the species' advantage to have a cub killed when a new male takes over a lion pride. It is not to the lionesses' advantage either! However, she is smaller than the male and often there is probably not much that she can do about it. Infanticide has evolved simply because the advantage to the male that practises it outweighs the cost to the female in resisting.

Not so long 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 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 think about the evolution of behaviour.

The most famous proponent of the idea that animals behave for the good of the group was 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.

Behaviour of advantage to individuals may be disadvantageous to the group

Theoretical considerations

Imagine a species of bird in which a female lays two eggs and there is no over-exploitation of the food resources. Suppose the tendency to lay two eggs is inherited. Now consider a mutant that lays three eggs. Since the population is not over-exploiting its food supplies, there will be plenty of food for the young and because the three-egg genotype produces 50% more offspring it will rapidly increase at the expense of the two-egg genotype.

Will the three-egg type be replaced by birds that lay four 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.
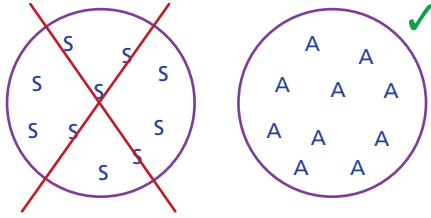
Group selection

Fig. 1.4 Wynne-Edwards' model of group selection. Groups of selfish individuals (S) over-exploit their resources and so die out. Groups of altruistic individuals (A), who do not over-exploit resources (e.g. by having fewer offspring than they could potentially raise) survive.

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 (Fig. 1.4).

In theory this can work, but it would require that groups are selected during evolution, with some groups dying out faster than others. In practice, however, groups usually do not go extinct fast enough for group selection to be an important force in evolution. Individuals will nearly always die at a faster rate than groups, so individual selection will be more powerful. In addition, for group selection to work populations must be isolated, such that individuals cannot successfully migrate between them. Otherwise there would be nothing to stop the migration of selfish individuals into a population of individuals all practising reproductive restraint. Once selfish individuals arrive, their genotype would soon spread. In nature, groups are rarely isolated sufficiently to prevent such immigration. So group selection as proposed by Wynne-Edwards is usually going to be a weak force and probably rarely very important (Williams, 1966a; Maynard Smith, 1976a). We revisit this topic in the final chapter.

Individual selection more powerful

Empirical studies: optimal clutch size

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 rather maximize their individual reproductive success. A classic example is the long-term study of the great tit (*Parus major*) in Wytham Woods, near Oxford, UK, started in 1947 by David Lack (Lack, 1966).

In this population the great tits nest in boxes (Fig. 1.5a) 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 re-trapping ringed birds. This intensive field study involves several people working full-time throughout the year, and it has been going on for over 60 years! Most pairs lay 8–9 eggs (Fig. 1.5b, bars). 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. 1.6a). 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 brood at the peak of nestling growth. In a survey of the sustainable

Clutch size in great tits …
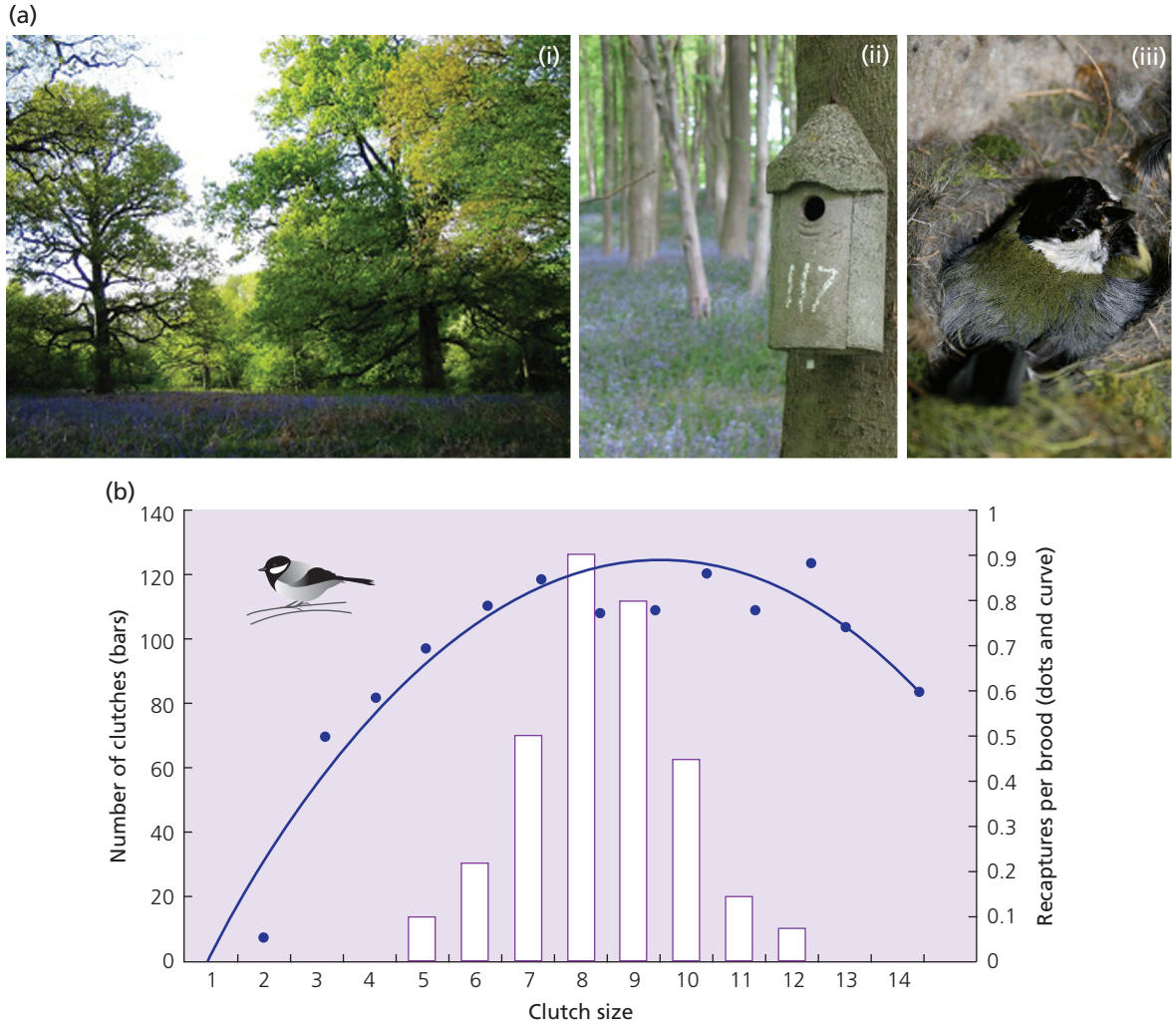
(a)

(b)

Fig. 1.5 (a) (i) Wytham Woods, Oxford, the site of a long-term study of great tit reproductive behaviour. Photo © Jane Carpenter (ii) A nest box. Photo © Ben Sheldon. (iii) Female great tit incubating a clutch. Photo © Sandra Bouwhuis (b) Bars: The frequency distribution of the clutch size of great tits in Wytham Woods. Most pairs lay 8–9 eggs. Curve and blue dots: Experimental manipulation of brood size shows that the clutch size that maximizes the number of surviving young per brood is slightly larger than the average observed clutch size. From Perrins (1965).

metabolic rates of animals, only two examples were found of animals working at more than seven times their resting metabolic rate: breeding birds and cyclists on the Tour de France cycle race (Peterson *et al.*, 1990).

The significance of nestling weight is that heavier chicks survive better (Fig. 1.6b). Therefore, an over-ambitious parent will leave fewer surviving young because it cannot feed its nestlings adequately. By creating broods of different sizes experimentally and allocating them at random to different nests, it was demonstrated that there is an

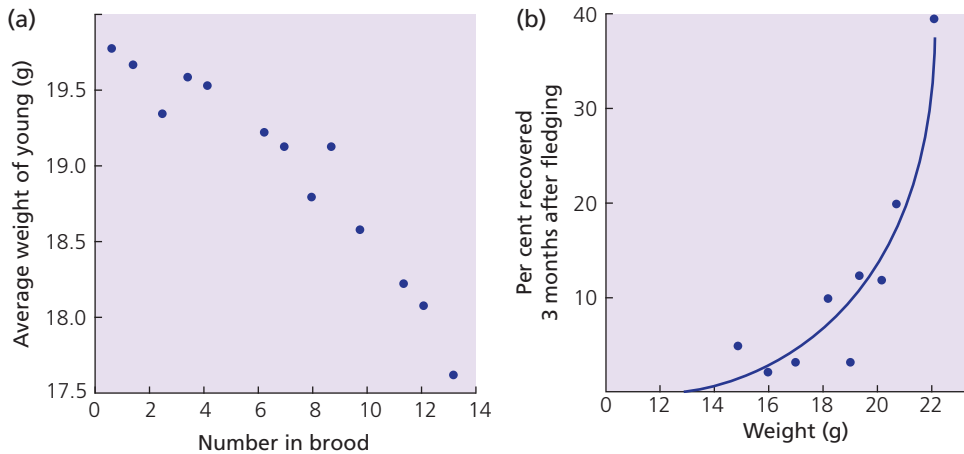**… is less than that predicted to maximize the number of surviving young per brood**

Fig. 1.6 Experimental manipulation of brood sizes in great tits. (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).

optimum to maximize the number of surviving young per brood from a selfish individual's point of view (Fig. 1.5b, curve). The most commonly observed clutch size is close to the predicted optimum but slightly lower. Why is this?

Two hypotheses for the mismatch between observed and predicted …

One hypothesis is that the optimum in Fig. 1.5b (curve) 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. If increased brood sizes are costly to adult survival, and hence chances of further reproduction, then the clutch size which maximizes lifetime breeding success will be slightly less than that which maximizes success per breeding attempt (Fig. 1.7). Box 1.1 gives a more general model for the optimal trade-off between current and future reproductive effort.

A second hypothesis for the lower than predicted clutch size is that when great tits are experimentally given extra eggs or chicks they may well be able to rear some extra young efficiently, but we have ignored the costs of egg production and incubation (Monaghan & Nager, 1997). A fairer test would be to somehow manipulate birds into laying extra eggs, rather than giving them extra eggs or chicks for free. If females were forced to pay the 'full cost' of laying and incubating the extra eggs, then this may reduce the predicted optimal brood size to maximize the number of surviving chicks per brood.

…. involve considering further trade-offs

Note that both hypotheses involve measuring further trade-offs. David Lack's predicted optimum (Fig. 1.5b, curve) involved the trade-off between offspring number and quality. Our first hypothesis for the mis-match between his prediction and the observed clutch size is that we need to consider, in addition, the trade-off between adult reproductive effort and adult mortality. The second hypothesis concerns another trade-off, that between investment in egg production and incubation versus chick care. As we shall see throughout this book, resources are limited and one of the main

themes of behavioural ecology is investigating how various trade-offs are solved by natural selection.

Marcel Visser and Kate Lessells (2001) measured the effects of these two extra trade-offs on great tit optimal clutch size by a clever experimental design (first used by Heany & Monaghan (1995) for studying clutch size in a seabird). In a nest-box population of great tits in the Hoge Veluwe, a large national park in The Netherlands, they had three experimental groups of females, each raising two extra chicks:

(i) *Free chicks*. Two extra nestlings were added to the nest, soon after the female's own brood hatched. These females, therefore, only had to raise two extra chicks.

(ii) *Free eggs*. Two extra eggs were added to the clutch on the day the female began to incubate her own clutch. These females, therefore, had to incubate two extra eggs as well as raise the two extra chicks.

(iii) *Full costs*. The female was induced to lay two extra eggs by removing the first four eggs of the clutch on the day they were laid (previous experiments had shown that removal of four led to two extra eggs being laid). These four removed eggs were kept in a bed of moss and were returned to the clutch before incubation began. So this third group had to lay the two extra eggs, as well as incubate them, and raise the two extra chicks, thus paying the full cost of an increased clutch size.

The results showed that the number of young produced who survived to breeding age (recruits) did not differ between the three treatments. Therefore, there was no support for the second hypothesis; *full costs* females produced just as many surviving young as those given free eggs or chicks. However, female survival *was* affected; *full costs* females had the lowest survival to the next breeding season, while *free chicks* females survived the best, with *free eggs* females having intermediate survival. These results, therefore, support the first hypothesis; there is a trade-off between increased reproductive effort and adult survival. When female fitness was calculated, *full costs* females had lower fitness than control females (who were left to raise the clutch size they initially chose; Fig. 1.8). Therefore, when the costs of both egg production and incubation are taken into account, the observed clutch size is optimal (at least in comparison with an increase in clutch size of two eggs).

Brood size manipulations are most easily done with birds, but similar studies with mice (König *et al*., 1988) and insects (Wilson, 1994) also suggest that reproductive rate tends to maximize individual success, though the trade-offs involved vary from case to case, and they are often tricky to measure.

Clutch size may vary 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 individual optimization is provided by Goran Högstedt's study (1980) of magpies, *Pica pica*,
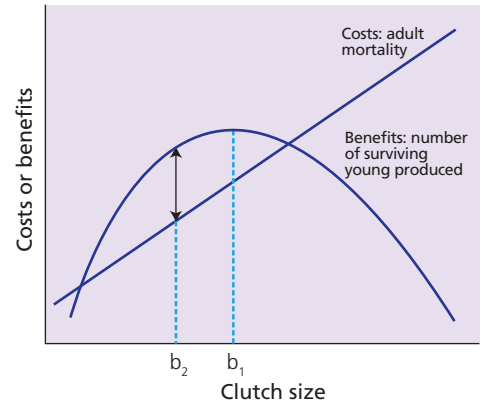

Fig. 1.7 The influence of adult mortality on the optimal clutch size. The number of young produced versus clutch size follows a curve, as in Fig. 1.5, with b_1 being the clutch size which maximizes the number of young produced per brood. Increased clutch size, however, has the cost of increased adult 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).

A trade-off between reproductive effort and adult survival to maximize lifetime success

Individuals may have different optima

BOX 1.1   THE OPTIMAL TRADE-OFF BETWEEN SURVIVAL AND REPRODUCTIVE EFFORT (PIANKA AND PARKER, 1975; BELL, 1980)

The more effort an individual puts into reproduction, the lower its chances of survival, 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, that is equal lifetime production of offspring (Fig. B1.1.1). 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 a 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.
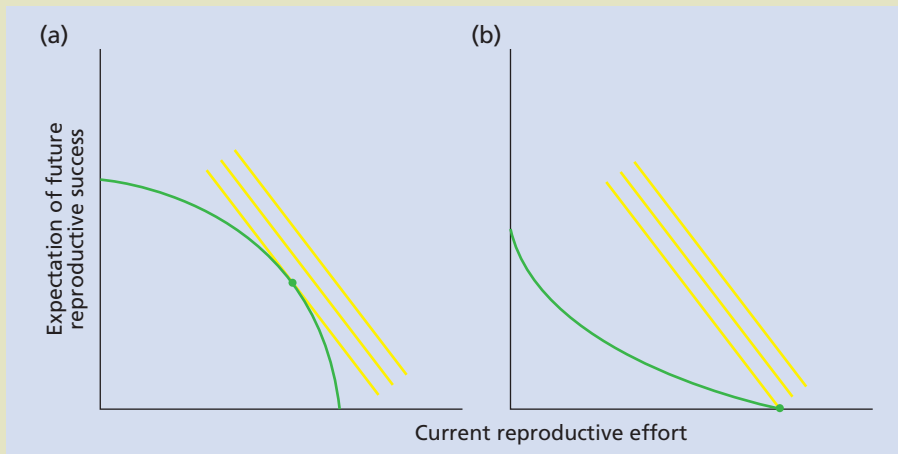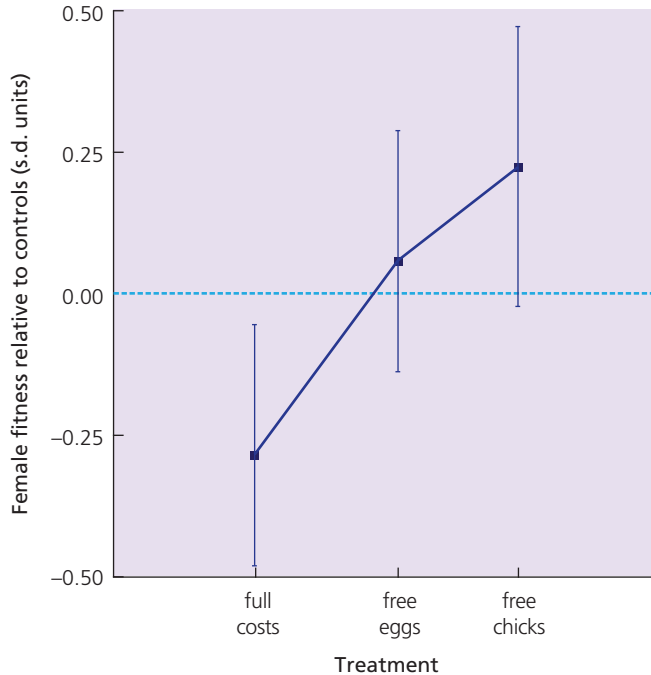

Fig. B1.1.1

Fig. 1.8 Fitness of female great tits in the experiment of Visser and Lessells (2001). Fitness was measured as (female survival to next breeding season) + (0.5 × number of offspring surviving to next breeding season). The logic behind this measure is that each offspring has only half the female's genes, so has half the 'genetic value' of the female herself. Female fitness is measured relative to controls (who raised the clutch size they initially laid) for three experimental groups who each had two extra chicks to raise, but with varying extra costs (see text). Females given *free* chicks or *free eggs* did better than controls but females forced to pay the *full costs* of laying and incubation had lower fitness than controls. From Visser and Lessells (2001).

breeding in southern Sweden. Observed clutch sizes varied from five to eight depending on feeding conditions in different territories. To test the hypothesis that some females laid only five eggs because this was the maximum number of young they could raise efficiently on their particular territories, Högstedt manipulated clutch sizes experimentally. He 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. 1.9). Variation 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; Tinbergen & Daan, 1990) and collared flycatchers (Gustafsson & Sutherland, 1988).
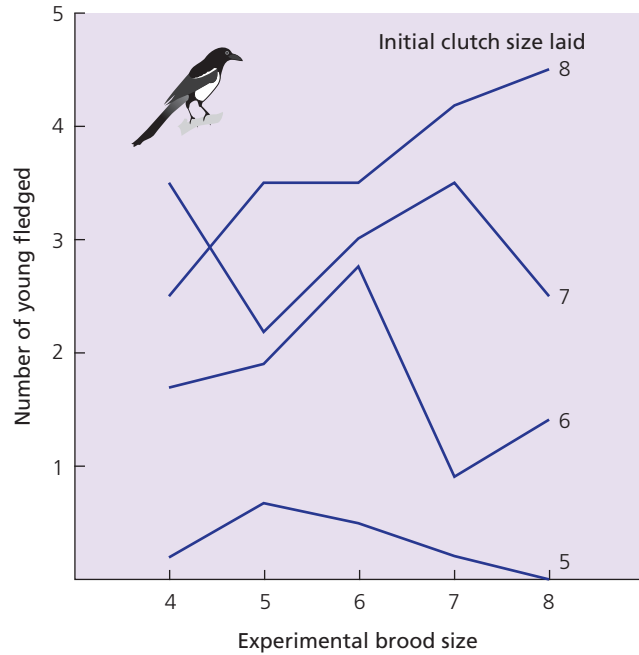
Fig. 1.9 Experiments on clutch size in magpies. Pairs that had initially laid 5, 6, 7 or 8 eggs were given experimentally reduced or enlarged broods. Pairs that had naturally laid large clutches did better with large broods and those naturally laying small clutches did better with small broods. From Högstedt (1980). Reprinted with permission from AAAS.

Phenotypic plasticity: climate change and breeding times

Reaction norms

The ability of a single genotype to alter its phenotype in response to environmental conditions is termed *phenotypic plasticity*. For example, we have just seen that clutch size is a phenotypically plastic trait which varies with season and food availability. When the phenotypic variation is continuous, the relationship between phenotype and the environment for each genotype is called a *reaction norm* (Fig. 1.10). There may be genetic variation in both the elevation of the line (the trait value) and its slope (the way the trait value changes in response to the environment). Recent studies of the earlier breeding of songbirds in response to climate change provide a good example of phenotypic plasticity. They also show how useful it is to study both proximate and ultimate explanations of behaviour together, hand in hand.

Warmer springs and earlier breeding in great tits

Over 47 years (1961–2007), the mean egg laying date of female great tits in the Wytham Wood population (near Oxford, UK) has advanced by about 14 days (Fig. 1.11a). The main changes have been from the mid 1970s, since when there has been a marked increase in spring temperatures (Fig. 1.11b). This has led to the earlier
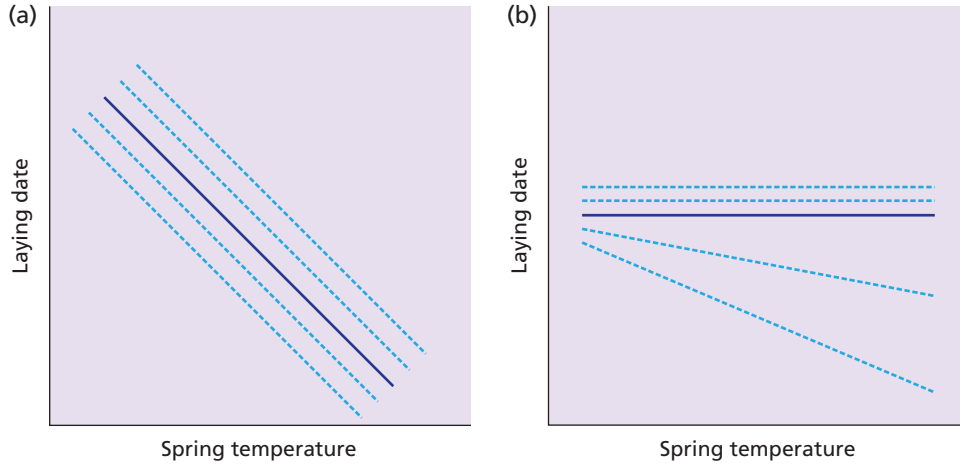
(a)

(b)

Fig. 1.10   Phenotypic plasticity in laying dates in response to spring temperatures. Dashed lines represent examples of reaction norms for different individual females, who may differ in their average laying date (elevation) or in their plasticity in response to spring temperatures (slope). In Wytham Woods, UK, the great tits respond as in (a), with no significant variation between females in plasticity and a strong average population response to temperature (solid line). In the Hoge Veluwe, The Netherlands, the great tits respond as in (b), with no significant average population response (solid line) but significant variation in individual female plasticity. After Charmantier *et al.* (2008). Reprinted with permission from AAAS.

emergence of oak leaves (*Quercus robur*) and of winter moth caterpillars (*Operophtera brumata*), which feed on the oak leaves and are a key food for nestling tits. The rates of change of egg laying date with temperature (Fig. 1.11c) and of caterpillar emergence with temperature (Fig. 1.11d) are similar, so the tits have closely tracked the temporal changes in food availability over almost five decades.

How have the tits managed to do this? For temperate breeding birds, an increasing photoperiod in the spring is the primary proximate cue that initiates gonadal growth and the hormonal changes involved in breeding. However, the response can be fine-tuned by other cues, such as temperature, food availability and social stimulation (Dawson, 2008). One possible explanation for the earlier breeding is that there has been micro-evolutionary change in the tit population, with selection favouring new genotypes with different thresholds of response to these proximate cues (e.g. breeding at shorter lengths of day). The other possibility is that earlier breeding has simply arisen through phenotypic plasticity, with no need for any genetic change.

Anne Charmantier, Ben Sheldon and colleagues have shown that this second hypothesis explains the response to climate change by the Wytham great tits. They analysed the laying dates of 644 individual females who had bred in three or more years. They found no significant variation among these individual responses to spring temperature, so all females had similar reaction norms (Fig. 1.10a). Furthermore, the slope of these individual responses was similar to that for the population as a whole

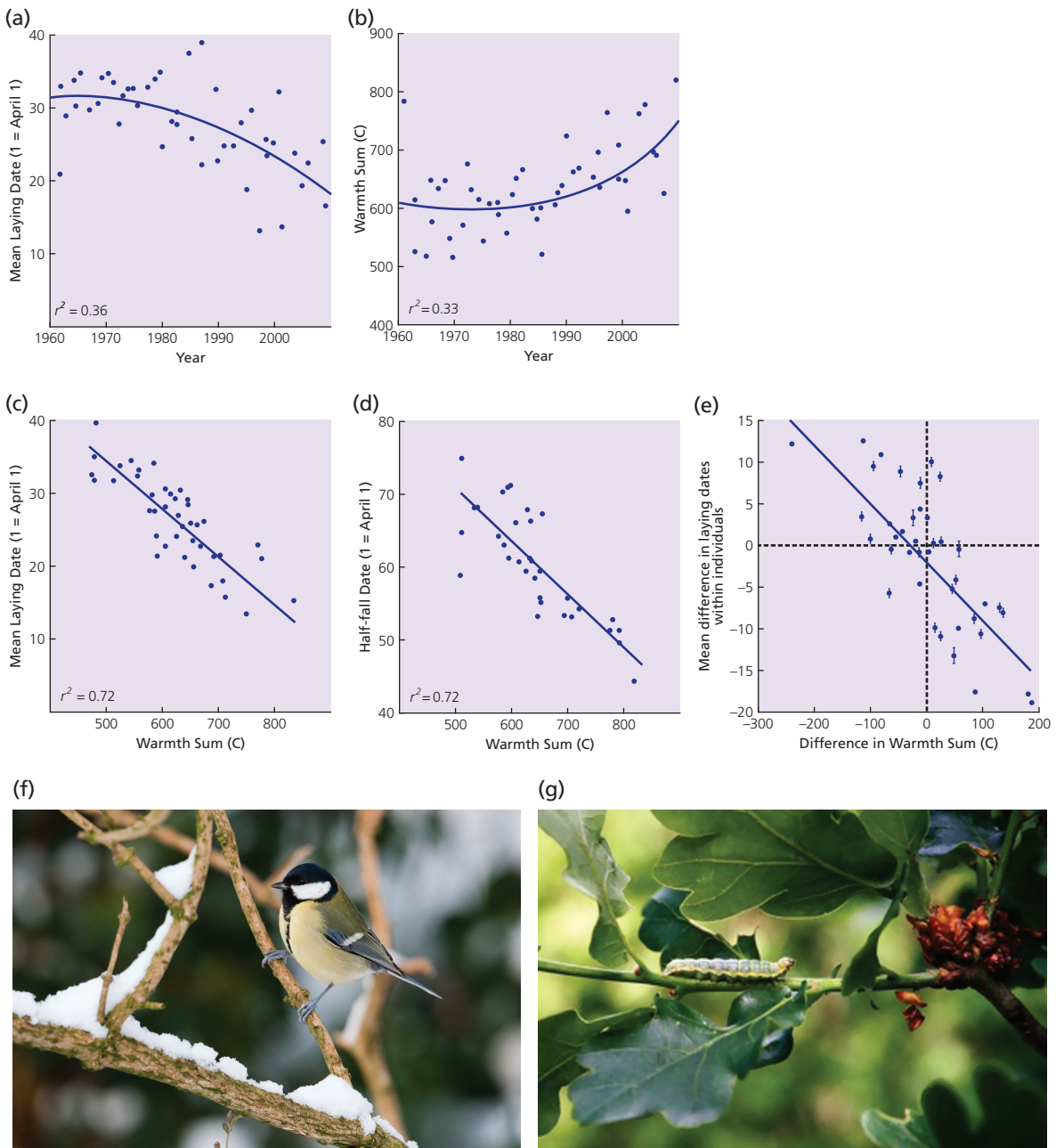**Genetic change or phenotypic plasticity?**

Fig. 1.11 (a) In Wytham Woods, UK, the mean laying date of great tits has become earlier, especially since the mid 1970s. (b) Spring temperatures have also increased, as measured by 'Warmth Sum', which is the sum of daily maximum temperatures between 1 March and 25 April (the pre-laying period). The rates of change in mean egg laying date with temperature (c) and caterpillar emergence with temperature (d) are similar. (e) Phenotypic plasticity in response of individual female great tits, measured as their difference in laying date in successive years plotted against the difference in spring warmth in the same pair of years. Figures a-e from Charmantier *et al* (2008). Reprinted with permission from AAAS. (f) Female great tit. Photo © Thor Veen. (g) Winter moth caterpillar on oak. Photo © Jane Carpenter.

(Fig. 1.11e). Therefore the population level change can be explained entirely by the magnitude of the plastic responses of individual females.

Studies of a great tit population in the Hoge Veluwe, The Netherlands, paint a very different picture (Visser *et al.*, 1998; Nussey *et al.*, 2005). Here, there has also been a similar environmental change during the last three decades (1973–2004), with warmer late spring temperatures and earlier emergence of the tits' caterpillar food supply. However, there has been no change in the tits' egg laying date, with the result that many of the Dutch birds are now breeding too late to catch the caterpillar peak for their hungry offspring. As a result, female lifetime reproductive success has declined over the study period (in contrast to the Wytham population, which is flourishing). Analysis of the variation shown by individual females over successive years, showed that (unlike the Wytham population) females varied in their phenotypic plasticity. Some responded little to annual variation in temperature whereas others showed a marked response (Fig. 1.10b). Furthermore, the variation in plasticity is heritable. In theory, then, the more plastic genotypes should now be favoured by natural selection.

Why do the Dutch and British tits differ? One possibility is that females in the two populations use different proximate cues to time their egg laying (Lyon *et al.*, 2008). For example, if only photoperiod was used as a cue, then individuals would not breed earlier in warmer springs. By contrast, if both birds and caterpillars responded to temperature, or some other common environmental cue, then individual tits would automatically track any yearly variation in caterpillar emergence.

Another possibility is that British and Dutch tits use the same cues but in Britain the cues are better predictors of the food supply that will be available to nestlings. In the Hoge Veluwe, over the last three decades there has been little change in early spring temperatures (when the adult tits are forming food reserves to breed) in contrast to the markedly warmer late spring temperatures, which influence the caterpillar food available to nestlings. The adult tits may, therefore, not have been able to predict the earlier food availability for their offspring (Visser *et al.*, 1998).

The conclusion is that we need to understand the proximate mechanisms used to time egg laying in order to predict how populations will evolve to cope with changing food supplies.

Behaviour, ecology and evolution

We can now summarize the main themes of this book.

Firstly, during evolution natural selection will favour individuals who adopt life history strategies that maximize their gene contribution to future generations. The optimization of clutch size in great tits provides a convincing quantitative test of this, but we shall see later in the book that having offspring is only one of the ways of passing genes on to the future. Another pathway is by helping close relatives to reproduce. One of the questions we shall ask is what factors influence which pathway individuals choose.

Secondly, because an individual's success at survival and reproduction depends critically on its behaviour, selection will tend to design individuals to be efficient at foraging, avoiding predators, finding mates, parental care and so on. Resources are limited, so there will always be trade-offs involved, both within and between these various activities. For example, will an individual avoid predation best by seeking the

safety of a group or by hiding away alone? The best place to feed may have the highest predation risk. How are these trade-offs solved by natural selection?

Thirdly, individuals are likely to have to compete with others for scarce resources. As we shall discover, conflict occurs not only between rivals for mates or territories, but also between members of a breeding pair and even between parents and their own offspring. How are such conflicts resolved? Can the outcome sometimes be cooperation rather than overt conflict?

Fourthly, individuals play their behaviour on an ecological stage. Different species live in different habitats and exploit different resources. This, too, is expected to influence an individual's best options. So we will also be exploring how ecological conditions influence how individuals behave.

We will show how the same basic theories can be applied to a wide range of organisms, from microbes to meerkats, and we will see the ingenuity required to design careful experiments to test the theories, both in the field and the laboratory. Most of all, we hope to show how ideas from behavioural ecology can help us to understand and appreciate the marvels of the natural world.

Summary

Behavioural ecology aims to understand how behaviour evolves in relation to ecological conditions, including both the physical environment and the social environment (competitors, predators and parasites). It is important to distinguish proximate factors, which explain how individuals come to behave in a particular way during their lifetime, from ultimate factors, which concern adaptive advantage in evolution. Natural selection works on genetic differences. Examples were discussed to illustrate how genetic differences cause differences in phenotype and behaviour: foraging, learning and courtship in *Drosophila*; foraging in honeybees; colour and mate/habitat choice in geese and mice; and migration strategies in the blackcap, which provide an example of a recent evolutionary change in behaviour.

Individuals are not generally expected to behave for the good of the group but rather to maximize their own gene contribution to future generations. Field experiments reveal that clutch size in great tits maximizes individual lifetime reproductive success. Life history trade-offs include those between quantity and quality of offspring within a brood, and between current and future reproduction.

Recent studies of how great tits have advanced their time of breeding in relation to climate warming provide a good example of phenotypic plasticity (the ability of a single genotype to produce different phenotypes in response to environmental conditions). They also show that a full understanding of evolutionary responses requires studies of proximate and ultimate factors to go hand in hand.

Further reading

The classic books by Niko Tinbergen (1974) and Bert Hölldobler and Edward O. Wilson (1994) convey the delight of watching and wondering in the field. The books by Richard Dawkins (1982, 1989) explain why evolution favours behaviour that benefits

individuals and genes, rather than species and groups. Reeve and Sherman (1993) provide a lucid discussion of the distinctions between Tinbergen's four questions and the inter-relationships between them. Scott-Phillips *et al.* (2011) discuss the distinction between proximate and ultimate questions about human behaviour. Robinson *et al* (2008) review genes and social behaviour. Pulido (2007) reviews the genetics and evolution of bird migration. Godfray *et* al. (1991) review clutch size. Both and Visser (2001) show how migrant birds, which breed in northern Europe, may be constrained in their responses to advanced springs on the breeding grounds due to climate change, because their migration from African winter quarters is triggered by day-length variation on the wintering grounds.

TOPICS FOR DISCUSSION

1. Is it possible to investigate the function of a behaviour pattern without understanding also its causation, development and evolution?

2. In this chapter it was concluded that infanticide had evolved because of its advantage to male lions when they take-over a pride. An alternative hypothesis is that it is simply the non-adaptive outcome of the mayhem involved when a new group of males takes over. How would you distinguish between these hypotheses?

3. Discuss how the production of a larger clutch size in one year could lead to decreased reproductive success of the parents in future years. How would you test your hypotheses?

4. Discuss the problems of investigating whether clutch sizes are 'optimal' from field studies. What would you conclude if your study showed that clutch size was sometimes apparently not optimal? (Read: Tinbergen & Both, 1999). Could rapid climate change lead to sub-optimal clutch sizes?