

Chapter 1

The Evolution of Behavioural Ecology

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1.1 Observations and questions

All natural history observations begin with a question. At first our curiosity may be satisfied simply by knowing the species name of the animal we are watching. Then we may want to discover what it is doing and to understand why it is behaving in a particular way. In 1978, we began the first edition of this book by asking the reader to observe a bird, such as a starling (*Sturnus vulgaris*), searching in the grass for food. The starling walks along, pausing every now and then to probe into the ground. Sometimes it succeeds in finding a prey item, such as a beetle larva, and eventually, when it has collected several prey, it flies back to the nest to feed its hungry brood.

For students of behavioural ecology, a whole host of questions come to mind as they observe this behaviour. The first set of questions concern the way the bird feeds. Why has it chosen that particular place to forage? Why is it alone rather than in a flock? What determines its choice of foraging path? 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 food and fly back to feed its chicks? Another set of questions emerges when we follow the starling back to the nest. Why has it chosen this site? Why this brood size? How do the two parent starlings come to an agreement over how much work each puts into offspring care? Why are the chicks begging so noisily? Are they each simply signalling their own degree of hunger or are they competing for food? Why such costly begging behaviour? If we observed the starling over a longer period of time then we may ask about what determines how much effort it puts into reproduction versus its own maintenance, about the factors influencing the timing of its seasonal activities, its choice of mate, and so on.

Behavioural ecology provides a framework for answering these kinds of questions. It combines ideas from evolution, ecology and behaviour and has emerged from five schools of thought, developed primarily in the 1960s and early 1970s. We discuss them in turn to provide a brief history of the subject and to show how the ideas have evolved in the last 20–30 years, and we point out how this book reflects recent developments.

1.2 Tinbergen's four questions

Tinbergen (1963) showed that there are four ways of answering the question 'why?' in biology. Returning to our starling, if we asked why it foraged in a particular way we could answer as follows.

- 1 In terms of *function*, namely how patch choice and prey choice contribute to the survival of the bird and its offspring.
- 2 In terms of *causation*, namely the proximate factors which caused the bird to select a foraging site or prey type. These may include cues to prey abundance such as type of soil or vegetation, or the activities of other birds.
- 3 In terms of *development*. This answer would be concerned with the role of genetic predispositions and learning in an individual's decision making.
- 4 In terms of *evolutionary history*, namely how starling behaviour has evolved from its ancestors. This answer might include an investigation of how the starling family has radiated to fill particular ecological niches and the influence of competition from other animals on the evolution of starling behaviour and morphology (e.g. bill size, body size).

Tinbergen's studies on gulls aimed to combine the four kinds of answer and he emphasized the need to study animals in their natural surroundings, namely those where their behaviour had evolved. He championed the use of the field as a natural laboratory for observations and controlled experiments and showed how ideas can be tested by collecting quantitative data on behaviour patterns (e.g. Tinbergen, 1953, 1972). Tinbergen's legacy is evident in current field studies of behaviour, many of which use simple experiments to measure the costs and benefits of traits. A good example is the classic manipulation experiments by Andersson and Moller to investigate mate choice in widowbirds and swallows, discussed by Ryan in Chapter 8.

However, early studies in behavioural ecology often focused on function and tended to ignore the other three questions. A caricature of behaviour studies in the 1930s is one where researchers imagined their animals as little machines blindly following fixed action patterns in responses to external stimuli. A caricature from the early days of behavioural ecology and sociobiology in the 1970s is the opposite extreme of regarding animals as scheming tacticians weighing up the costs and benefits of every conceivable course of action and always choosing the best one. Current work is leading to an intermediate position. While we expect selection to favour mechanisms that maximize an individual's fitness, we must recognize that mechanisms both constrain and serve behavioural outcomes.

A good example to illustrate this point is Lotem's recent studies of hosts come to recognize a cuckoo egg in their nest. The cuckoo, *Cuculus canorus*, is a brood parasite which exploits various small birds as hosts to raise its offspring. The female cuckoo lays just one egg per host nest. The cuckoo chick hatches first, whereupon it ejects the host's eggs over the side of the nest, becoming the sole occupant. Given the cost of parasitism, it is not surprising

that many hosts have evolved defences such as rejection of odd eggs in their nest. Nevertheless, the puzzle is that egg rejection rarely reaches 100% in the host population and, furthermore, hosts never reject the cuckoo chick. A consideration of mechanisms may help to solve both puzzles. Experiments show that the defence mechanism used by hosts involves learning the characteristics of their own eggs the first time they breed and then rejecting eggs which differ from this learned set (Lotem *et al.*, 1995). This makes it unlikely that the host population will evolve 100% rejection of cuckoo eggs because hosts which are parasitized during their first breeding attempt will learn the cuckoo egg as part of their own set. Nevertheless, the learning rule works quite well and leads hosts to reject many parasite eggs. At the chick stage, however, a learning rule does less well than a rule 'accept any chick in my nest'. This is because there is a considerable cost of misimprinting: any host parasitized in its first attempt would learn only the cuckoo chick as its own and would then subsequently reject its own young in future, unparasitized, broods (Lotem, 1993). The main message from this study is that it is not very fruitful to discuss the evolution of 'rejection' without specifying the mechanisms, because these will determine the costs and benefits involved. Studies of mechanism and function must go hand in hand.

In 1975, Wilson predicted the demise of ethology, with mechanisms becoming the domain of neurobiology, and function and evolution the domain of sociobiology. This prediction was fulfilled until recent years, when there has been a welcome renewed interest in linking mechanism and function. We have marked this change by devoting the first section of this volume to this fruitful interchange. For example, Giraldeau (see Chapter 3) shows how research on foraging behaviour has stimulated new questions about learning and memory mechanisms, and Sherman *et al.* (see Chapter 4) point out common features of recognition mechanisms of kin, mates and predators and discuss their functional significance.

1.3 Ecology and behaviour

Even before Darwin, biologists often interpreted morphological adaptations in relation to the environment in which the species lived. Darwin's achievement was to show how these could arise without a Creator. Once the early ethologists, such as Lorenz and Tinbergen, had demonstrated that behaviour patterns were often as characteristic of a species as its morphological features, attempts were made to correlate differences between species in behaviour with differences in ecological factors, such as habitat, food and predation. A pioneering study was that by Cullen (1957), who was a student of Tinbergen. She interpreted the reduced anti-predator behaviour of kittiwake gulls, *Rissa tridactyla*, compared to the ground-nesting gulls, in relation to their safer nest sites on steep cliffs. Two other early studies were those by Winn (1958), who linked the reproductive behaviour of 14 species of darter fish (Percidae) to their ecology, and by Brown

and Wilson (1959), who related the colony size and structure of dacetine ants to their feeding habits.

Crook's (1964) study of weaver birds (Ploceinae) has become established as the model for this approach. Crook showed how differences between species in food and predator pressure affect a whole host of adaptations, including nesting dispersion (colonies versus territories), feeding behaviour (solitary versus flock) and mating systems (monogamy versus polygamy). This comparative method was soon extended to other groups, including primates (Crook & Gartlan, 1966), other bird species (Crook, 1965; Lack, 1968), ungulates (Jarman, 1974), carnivores (Kruuk, 1975) and coral reef fish (Fricke, 1975).

The comparative approach remains influential today, the main advances being in methodology, particularly the quantification of behavioural and ecological traits, the use of multivariate statistics to tease out confounding variables and methods for identifying independent evolutionary events (Clutton-Brock & Harvey, 1984). It is now agreed that the ideal way to carry out a comparative analysis is to reconstruct a phylogenetic tree of the group under study and to use this as the basis for independent comparisons. Phylogenies not only provide a way of identifying independent evolution but also show the sequence in which traits have evolved within a group. With molecular phylogenies there is also the potential to measure the time-scale of evolutionary change. This new approach to Tinbergen's fourth question is one of the major developments in recent years and is discussed by Harvey and Nee in Chapter 14.

1.4 Economic models of behaviour

Many early studies in ethology recognized that behaviour patterns involve costs as well as benefits. For example, Tinbergen *et al.* (1963) showed that removal of the egg-shell after hatching reduced predation of black-headed gull, *Larus ridibundus*, nests (the egg has a conspicuous white interior). But, leaving newly hatched chicks unattended is costly too, which probably explains why the parent delays egg-shell removal until the chicks have dried out and become less vulnerable to attacks from neighbouring gulls.

The pioneer in the use of mathematical models in ecology to quantify these kinds of trade-offs was Robert MacArthur, who first applied the idea of optimal choice in the context of foraging behaviour (e.g. MacArthur & Pianka, 1966; MacArthur, 1972). The argument for using optimality models in behavioural ecology is that natural selection is an optimizing agent, favouring design features of organisms which best promote an individual's propagation of copies of its genes into future generations. Behaviour patterns clearly contribute to this ultimate goal, so we expect individuals to be designed as efficient at foraging, avoiding predators, mate choice, parenting, and so on. Optimality models have three components: (i) an assumption about the choices facing the animal (e.g. prey type); (ii) an assumption about what is being maximized (e.g. rate of energy gain); and (iii) an assumption about constraints (e.g. bill size, searching

speed). For example, from a knowledge of prey available and morphological constraints, we could predict how our starling should select prey so as to maximize its rate of food delivery to its brood. If the model fails to predict the observed behaviour, we can then use the discrepancies to help identify which of our assumptions was incorrect. Classic early studies include work by Schoener (1971) and Charnov (1976a,b) on prey choice and patch choice by foragers, and Parker's study of copulation time in the yellow dungfly, *Scatophaga stercoraria* (Parker, 1970a; Parker & Stuart, 1976).

The optimality approach has met with some criticism but in our view it remains the most powerful method for studying the design of behaviour (for discussion see Maynard Smith, 1978; Stephens & Krebs, 1986). Perhaps the main problem facing a behavioural ecologist is that the animals under study are clearly faced with trade-offs not just within a particular activity but also between activities. The starling has to find food, keep an eye out for predators and return to the nest to keep its brood warm, for example. In Chapter 5, Cuthill and Houston discuss techniques for considering how different activities combine to influence fitness. In particular, they show how dynamic programming can be used to model sequences of behavioural choices.

1.5 Evolutionarily stable strategies

An animal's environment does not consist solely of places to feed, nest, shelter and hide from predators. There is also a living environment of competitors. Often an individual's best choice will be influenced by what these competitors are doing. Thus, the best place for our starling to feed will depend on where the other starlings go, the best strategy to adopt in a fight will depend on what the opponent does, and the best sex ratio for an individual to produce in its offspring will depend on the population sex ratio. Early studies to recognize this important point include Fisher's (1930) explanation for why parents expend equal resources on male and female progeny, Hamilton's (1967) analysis of stable sex ratios under local mate competition, Parker's (1970c, 1974b) field study of how male dungflies distribute themselves across different mating sites and work by Fretwell and Lucas (1970) on habitat choice by birds. All these studies analysed the problem in terms of which choices would produce an equilibrium distribution in the population.

Maynard Smith's (1972, 1982) concept of the evolutionarily stable strategy (ESS) is now widely accepted as the way of analysing decision making where the payoffs are frequency dependent. A strategy is an ESS if, when adopted by most members of a population, it cannot be invaded by the spread of any rare alternative strategy. This idea has been influential in analysing many problems in behavioural ecology including fighting behaviour and communication (see Chapter 7), mating systems (see Chapter 6) and cooperation and conflict in social groups (see Chapters 9 and 11). In many cases no single strategy is an ESS, so one of the main messages for field workers has been to expect variability

in behaviour. Sometimes the variability is between individuals, so there is a polymorphism in the population. Hamilton's (1979) study of dimorphic males in fig wasps provided an early classic example of stable alternative strategies within a species. For recent examples, see Shuster and Wade (1991), Lank *et al.* (1995) and Sinervo and Lively (1996). More often, individuals vary in their behaviour depending on what their competitors do. A rule 'go to the patch with the greatest number of worm casts' would be fine for a bird if it was the only forager, but in the presence of competition this may not be the best thing to do. The behavioural ecologist's task here is to consider what would be the stable decision rules (see Chapter 3 by Giraldeau for a discussion of this problem).

ESS models have been particularly useful in studies of signalling systems. In many cases animal displays seem at first sight to be unnecessarily extravagant, for example the stretching, gaping and calling of young birds as they beg for food or the energetic dancing of males on a lek as they attempt to attract a female for mating. Zahavi's (1975, 1977a) handicap principle proposed that signals are costly to prevent cheating. The key here is that there are often conflicts of interest between signallers and receivers: it pays offspring to beg for more than their fair share of food and it pays even poor-quality males to attract mates. Zahavi suggested that if signals were costly then this would enforce honesty so that, for example, only really hungry chicks would gain from begging and only the best-quality males could perform impressive displays. ESS models by Grafen (1990a,b) have confirmed that such costs produce a signalling equilibrium. This theory is now stimulating empirical work on the costs and benefits of signalling in relation to individual quality, and Johnstone (see Chapter 7) reviews these studies together with more recent theoretical developments.

1.6 Kinship, social evolution and breeding systems

Up to the mid-1960s, many interpretations of animal social behaviour were in terms of how it was of advantage to the group. Wynne-Edwards (1962) proposed that social behaviour was an adaptation for regulating animal populations and many ethologists also used group selection to explain behaviour. For example, Tinbergen (1964) interpreted the mobbing of a hawk by a group of birds as behaviour which, although of danger to the individual, was advantageous to the group. He argued that 'only groups of capable individuals survive — those composed of defective individuals do not, and hence cannot reproduce properly. In this way the result of cooperation of individuals is continually tested and checked, and thus the group determines, ultimately, through its efficiency, the properties of the individual'.

Group selection was criticized most cogently by Williams (1966) and Lack (in an Appendix to his 1966 book). They showed that clutch size and also

many social interactions enhanced an individual's fitness and argued that adaptations evolve for individual benefit, not for the benefit of a group. This left the problem of altruism, behaviour which increased the fitness of others at a cost to the altruist's own personal reproduction. The key insight to understanding the evolution of altruism was provided by Hamilton (1964a,b). He argued that individuals can pass copies of their genes on to future generations not only through their own reproduction (direct fitness) but also by assisting the reproduction of close relatives (indirect fitness). Hamilton's now famous rule specifies the conditions under which reproductive altruism evolves and there is good evidence, especially from insects (see Chapter 9) and social vertebrates (see Chapters 10 and 11), that kinship provides the key to understanding altruistic behaviour. The huge interest in cooperative breeding during the last 20 years is largely inspired by Hamilton and is a good example of how empirical work is often driven by advances in theory.

Further impetus to studies of social systems came from pioneering papers by Parker and Trivers. Parker (1970a) recognized the importance of multiple mating for the evolution of reproductive behaviour and coined the term 'sperm competition' for sexual competition after mating, when sperm from different males compete for fertilization of a female's ova. Trivers laid the foundations for theories of conflicts in family groups (see Chapters 9 and 10), including male-female conflict and parent-offspring conflict (Trivers, 1972, 1974; Trivers & Hare, 1976). He emphasized the importance of the earlier conclusions of Bateman (1948) that different factors limit reproductive rates in males and females. Females tend to invest more in offspring and their reproductive rate is usually limited by resources. A male, on the other hand, has the potential to father offspring at a faster rate than a female can produce them. For males, therefore, reproductive success is limited more by access to females. Trivers argued that females should be more choosy in mating while males should practice a 'mixed reproductive strategy', both guarding their mates and also attempting to gain extrapair matings. Parker (1979, 1984b) also emphasized the conflict between the sexes, and both he and Maynard Smith (1977) used ESS models to analyse how these may be resolved.

In the last decade, detailed behavioural observations combined with molecular measures of parentage (e.g. DNA fingerprinting) have confirmed the importance of sperm competition and sexual conflict. This has revolutionized our view of mating systems. Just compare, for example, Lack's (1968) conclusion 30 years ago that monogamy predominates in birds because 'each male and each female will leave most descendants if they share in raising a brood' with the current evidence for widespread mixed paternity and sexual conflict (see Chapter 6). While it is clear that males compete for mates and females are indeed choosy, there is still vigorous debate about exactly what benefits females gain from their choice (see Chapter 8).

1.7 Critical views

Behavioural ecology has been criticized on a number of grounds during the past 20 years, the main points being as follows.

1.7.1 Determinism

Lewontin and colleagues (Lewontin et al., 1984; Lewontin, 1991) have interpreted the position of behavioural ecologists as implying genetic determinism. Statements such as '...a gene for altruism...' could be read as meaning that if an individual carries a certain gene or combination of genes it immutably and irrevocably behaves in a particular way. This would be biologically unsound, since the adult phenotype depends on complex interactions between genes and environment during development. It could also, Lewontin and colleagues argued, be open to an ideological interpretation in which social policies were built around the assumption that humans are purely products of their genetic heritage. Although it would be fair to say that behavioural ecologists have generally underplayed the complexities of behavioural development, the phrase '...a gene for...' is never used to imply genetic determinism, but rather as shorthand for '...genetic differences between individuals that are potentially or actually subject to selection'; in other words it implies gene selectionism not genetic determinism (Dawkins, 1982).

1.7.2 Panglossianism

A parody of behavioural ecology (and of neo-Darwinism in general) is that every last detail of any organism's behaviour, anatomy, physiology and so on can be explained by natural selection. For example the fact that carrots are orange and parsnips white. Gould and Lewontin (1979), in a classic article, coined the phrase 'The Panglossian paradigm', referring to Dr Pangloss in Voltaire's *Candide*, who took the view that everything was always for the best. According to its critics, the pure adaptationist approach is flawed for two reasons. First, it ignores the fact that evolution is a historical process influenced by chance, and some of the outcomes would be quite different if the video of life were played again (Gould, 1989). Differences between species or phyla may have no 'logic', they may just be the one chance outcome out of a huge range of possibilities. Second, at any one moment in time, the degree of perfection of adaptation of behaviour, physiology and so on are constrained by many factors such as developmental flexibility, historical accident and interactions between genes. While these criticisms do not undermine the value of a Darwinian framework as a powerful device for analysing and predicting behaviour, they are reflected in the fact that in this edition of the book we have included greater emphasis both on the analysis of historical events in evolution, increasingly

possible because of new phylogenetic data, and on the constraints that limit adaptation here and now.

1.7.3 Anthropomorphism

Kennedy (1992), in a thoughtful and detailed critique of behavioural ecology, points to the dangers of using (often anthropomorphic) linguistic shorthand to describe functional categories of behaviour. One of his key points is that the use of functional labels such as 'foraging', 'mate searching' and 'parental allocation' tend to become substitutes for a proper analysis of what is actually going on and may even encourage anthropomorphic interpretations of behaviour. For instance, a behavioural ecologist interested in 'honest signalling' (itself a dangerously anthropomorphic term!) between nestlings and parents in a particular bird species might analyse in a model, or by experiments, whether or not '...parents allocate resources in response to the need of individual nestlings...' Kennedy would argue that, in fact, parents respond to stimuli, including those emitted by the offspring, and that this is what determines the pattern of feeding. The terms 'allocation' and 'need' are, in effect, terms related to functional considerations of optimal reproductive strategies and should not be taken to constitute causal explanations of behaviour.

Kennedy's critique recalls the distinction between two of Tinbergen's four questions, function and causation, and it also serves as a reminder that in carrying out experimental manipulations of behaviour one can normally only determine the stimuli to which animals respond, not the functional reasons for a response, which are inferred from the logic of natural selection.

The main lessons for behavioural ecologists are these.

- 1 That functional models should not be taken to imply particular mechanisms or decision rules (in analyses of 'tit-for-tat' as a model of cooperation, the metaphor of the model has been interpreted literally by some authors to mean that animals play the actual game originally modelled by Axelrod and Hamilton — see Chapter 11).
- 2 That care should be taken in experimental analyses of functional models not to conflate manipulation of the stimuli to which animals respond, for example prey size or tail length, with the Darwinian interpretation of adaptation.
- 3 That functional labels should not substitute for a full analysis of the causes of behaviour.

1.8 Looking ahead

Sam Goldwyn neatly summarized the dangers of predicting: 'Never prophesy, especially about the future.' However, the changes signalled by the new emphases in this edition of *Behavioural Ecology* coincide with a change in the

nature of the subject. As we have mentioned earlier, Wilson's (1975) predicted fragmentation of the subject of ethology into functional and causal aspects is not happening; what is now emerging is a new form of integrated study of behaviour. In order for this to flourish, one of the keys will be to embrace the powerful armoury of techniques, from gene splicing to magnetic resonance imaging that have transformed other areas of biology.