Second edition

An Introduction to Behavioural Ecology

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SECOND EDITION

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Contents

Introduction

This brief introduction describes the organization and contents of our book. The book is about the survival value of behaviour. We call this subject 'behavioural ecology' because the way in which behaviour contributes to survival and reproduction depends on ecology. If, for example, we want to answer the question 'How does living in a group contribute to an individual's survival?', we have to start thinking in terms of the animal's ecology; the kind of food it eats, its enemies, its nesting requirements and so on. These ecological pressures will determine whether grouping is favoured or penalized by selection. Behavioural ecology is not only concerned with the animal's struggle to survive by exploiting resources and avoiding predators, but also with how behaviour contributes to reproductive success. Much of the book is therefore about competition between individuals for the chance to reproduce and pass on their genes to future generations.

The book emphasizes the theoretical background to each subject discussed, but we prefer to illustrate the theory with examples after a very brief general introduction, rather than developing long, abstract, theoretical arguments. Although none of the ideas we have used are difficult to understand we have placed some of the more complicated arguments and details in boxes which can be ignored if the reader is in a hurry.

Chapter 1 is a general introduction to the book, in which we distinguish between different kinds of questions that one can ask about behaviour. In particular we emphasize the difference between questions about survival value or function and those concerned with causal mechanisms. We show that natural selection should favour individuals who are best able to propagate their genes to future generations.

In chapter 2 we discuss how to test hypotheses for the adaptive advantage of behaviour. One method is comparison among species. The rationale here is that differences between species in behaviour can be correlated with differences in their ecology. From these correlations, inferences can be drawn about the adaptive significance of behavioural traits. We illustrate this approach with reference to social organization in weaver birds, antelope and primates. The second method is to perform experiments, for example to change behaviour and

measure the consequences this has for the individual's chances of survival and for its reproductive success.

In chapter 3 we focus on the individual. Animals are viewed as making 'decisions' between alternative courses of action and the decisions can be analysed in terms of their costs and benefits. A powerful tool in this approach is optimality theory, which allows us to test hypotheses about the importance of various costs and benefits by predicting their effects on the animal's decision rules. By considering the basic decisions underlying behaviour patterns, we show how the same models can be used to understand what at first sight seem very different problems, such as feeding and searching for mates. Chapter 4 looks at decisions over evolutionary time, and how these change during arms races between predators and prey, and brood parasites and hosts.

In the next three chapters we consider how individuals should behave when they have to compete with others for scarce resources such as food, territories or mates. We discuss how competitors should be distributed in relation to resource distribution and abundance (chp. 5) and the costs and benefits of living in groups (chp. 6). In chapter 7 we introduce the idea of game theory as a technique for analysing how individuals behave in contests for resources.

Chapters 8, 9 and 10 are concerned with sexual reproduction. A consideration of the basic differences between males and females leads to the idea that members of one sex (usually male) may compete for access to members of the other (chp. 8). This is the theory of sexual selection. The differences between male and female also suggest that the interests of the two sexes during reproduction often differ (the theory of sexual conflict). Chapter 9 discusses how these battles within and between the sexes are influenced by ecology. Here we rely heavily on the comparative approach, correlating differences between species in sexual strategies with differences in ecology. From differences between species we turn to differences between individuals (chp. 10). We introduce the idea that different individuals within a species sometimes adopt different sexual strategies. These differences may be related to age or size, or they may simply be equally profitable, alternative, ways of achieving the same end.

In chapter 11 we examine how altruistic behaviour can evolve. We then illustrate the theoretical arguments with reference to 'helpers'; individuals that help others to rear young instead of producing their own. Chapter 12 deals with birds, mammals and fish, and chapter 13 is devoted entirely to the social insects, where helping reaches its most sophisticated

level of development. Many of the earlier chapters refer to communication as a behavioural mechanism of competition for resources and social interaction. In chapter 14 we tie together these threads in a general discussion of animal signals. We follow the pattern set in earlier chapters by considering both ecological constraints and intraspecific selection pressures. In the final chapter we reassess the view that the survival value of behaviour can be understood within a neo-Darwinian framework using methods such as optimality models and game theory.

Finally a word about the style of presentation. We generally use convenient and informal shorthand rather than traditional formal scientific style. A phrase such as 'Offspring are selected to demand more food than the parent wants to give' is short for 'During the course of evolution selection acting on genetic differences in the begging behaviour of offspring will have favoured an increase in the intensity of begging. This increase will have been favoured to the extent where the level of begging by any individual offspring exceeds the optimum level for the parent'.

Some readers may wonder whether our informal shorthand, together with catchy descriptive labels for various behaviour patterns such as 'manipulation' and 'sneaker', are a sign of sloppy thinking. There is no doubt that loose terminology can indicate imprecise thinking and half-formulated ideas. But it is equally easy to conceal woolly arguments behind an obfuscating screen of scientific jargon. We have used a simple direct style in order to make our arguments clear and not because behavioural ecology is a woolly subject. This point is nowhere better illustrated than by George Orwell in his brilliant essay 'Politics and the English Language' (1946). He translates the following well-known verse from *Ecclesiastes*, into modern English. 'I returned and saw under the sun, that the race is not always to the swift, nor the battle to the strong, neither yet bread to the wise, nor yet riches to men of understanding, nor yet favour to men of skill; but time and chance happeneth to them all.'

And now the translation.

'Objective consideration of contemporary phenomena compels the conclusion that success or failure in competitive activities exhibits no tendency to be commensurate with innate capacity, but that a considerable element of the unpredictable must invariably be taken into account.'

This translation is not only tired and ugly, lacking the fresh, vivid imagery of the biblical passage, but it replaces precise illustrations with woolly generalization. While we cannot

hope to emulate the clarity and brilliance of the writer of *Ecclesiastes*, or indeed of George Orwell, we hope we have avoided the worst excesses of the Orwellian parody and presented our ideas in simple but precise language.

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 sunbirds defend territories containing 1600 flowers 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 sometimes 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 take-over 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

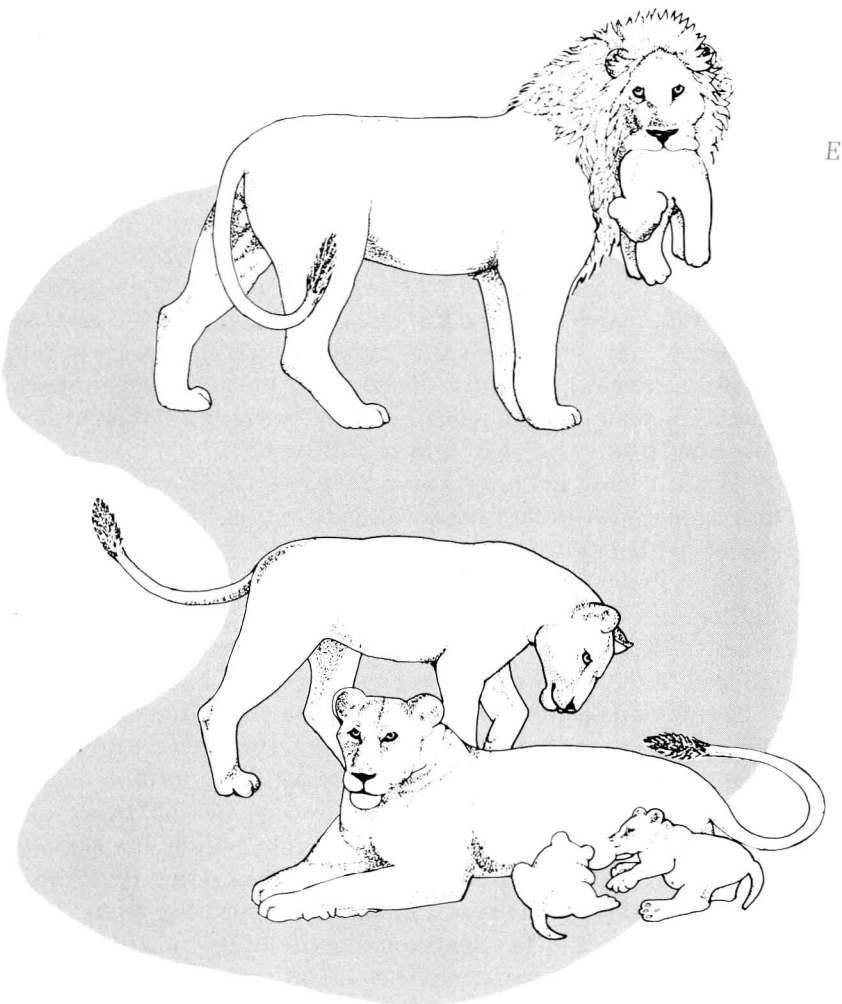

Fig. 1.1. Top: when a new male takes over a lion pride, he kills the young cubs fathered by the previous males. Bottom: a female suckles her sister's cub alongside her own.

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).

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 thoughout 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