

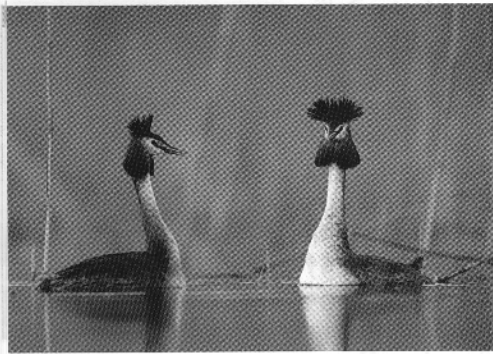


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Preface

In this Preface, we summarise the history and organisation of this book. The previous editions, by John Krebs and Nick Davies (1981, 1987, 1993) celebrated the early years of behavioural ecology. Our aim was to understand how behaviour evolves in the natural world. This requires links between studies of behaviour, evolution and ecology. The link with evolution is central because we expect natural selection to favour those behaviour patterns which maximise an individual's chances of surviving and passing copies of its genes on to future generations. The link with ecology comes in because ecology sets the stage on which individuals play their behaviour, so the best way to behave depends on ecological selection pressures, such as the distribution in space and time of food, enemies and places to live. The social environment will be important too, because individuals will often have to compete for scarce resources. So we need to consider how behaviour evolves when there are social interactions, with the potential for both conflict and cooperation.

This new edition celebrates a maturing and flourishing field, with exciting new links being forged with other disciplines. We now have three co-authors. John was an adviser for Nick's doctorate research in Oxford and Nick, in turn, lectured to Stu in undergraduate courses in Cambridge. So we span three (short!) academic generations and we have all enjoyed learning from each other during the preparation of this book. All the chapters have been heavily revised or completely reorganised and re-written to incorporate the many new ideas and examples which have emerged since the last edition - in some cases overturning what used to be the conventional wisdom. The central themes remain: a reductionist approach to consider the costs and benefits of decision making and how trade-offs are resolved by selection; a "gene's eye" view of behaviour; and a game theoretic approach to analyse the resolution of conflicts of interest. John and Nick remember the early days when Bill Hamilton, Robert Trivers and John Maynard Smith began to explore the ideas of kin selection, family conflicts and game theory for the analysis of conflict resolution, and when Richard Dawkins was testing drafts of *The Selfish Gene* as undergraduate lectures in Oxford. It is exciting to see how these ideas have evolved to stimulate the new research we discuss here. Throughout the book, we emphasise the theoretical background, but we prefer to

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develop the theory with examples rather than with abstract arguments. Some of the more complicated arguments are presented in boxes.

Chapter 1 begins with “watching and wondering” as we introduce how to frame different kinds of questions about behaviour. We then describe field experiments on clutch size, which show that individuals tend to maximise their lifetime reproductive success. Because an individual’s survival and reproductive success depends critically on its behaviour, selection is expected to design individuals to be efficient at feeding, avoiding predators, finding mates, and so on.

In Chapter 2 we discuss how to test hypotheses for the adaptive advantage of behaviour. One method is comparison among species, in effect analysing the results of evolutionary “experiments”, correlating differences between species in behaviour with differences in ecological and social selection pressures. There have been recent improvements in methodology, using phylogenies to identify independent evolutionary transitions and the order in which traits change. The second method, pioneered by Niko Tinbergen, is to perform experiments, for example to change behaviour and measure the consequences for an individual’s survival and reproductive success.

In Chapter 3, we focus on individual “decision making” between alternative courses of action. We show how optimality models can be used to predict decision rules, and how the same basic models can often be applied to what at first sight seem very different problems, such as feeding and searching for mates. We discuss the roles of social learning and teaching in the development of individual decision making, and use examples from food storing to explore the links between behavioural ecology, cognition and neuroscience. Chapter 4 considers decisions over evolutionary time, and how these change during arms races between predators and prey, and brood parasites and hosts.

The next two chapters consider how individuals should behave when they have to compete with others for scarce resources. Chapter 5 introduces a game theoretic approach to contest behaviour and shows that the outcome is often variability in the population, as individuals distribute across different habitats in space and time, or choose alternative strategies or tactics as they compete for food and mates. We also discuss the concept of animal personalities, a current growing field of research. In Chapter 6, we review the costs and benefits of group living, particularly in relation to foraging and avoiding predation. Recent studies have shown how local decision rules made by individuals can have remarkable consequences for group dynamics, leading to spectacular coordinated movements in bird flocks, fish shoals and ant trails.

The next four chapters are concerned with sexual reproduction. Chapter 7 shows that fundamental differences between the sexes in gamete size and parental investment often leads to males competing for females, either by force or by charm (Darwin’s theory of sexual selection). Females may choose males based on the resources they provide or the genetic benefits for their offspring. There is often sexual conflict and this continues after mating (sperm competition and female choice of sperm). Chapter 8 reviews parental care across the animal kingdom, and three inter-related conflicts: between male and female parent over who should care, and how much care to provide; between siblings; and between parents and their offspring. We consider the theory and evidence for each of these conflicts and distinguish between “battleground” models (which define the conflict) and “resolution” models (which explore the outcomes).

In Chapter 9, we show how different mating systems emerge depending on the economics of parental care and mate defence. The use of DNA profiles to measure

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parentage has now become routine and has revolutionised our view of family life, revealing (for example) that social monogamy does not necessarily mean genetic monogamy. Chapter 10 examines sex allocation: the problem of how a parent should divide its investment between male and female offspring. Sex allocation in hymenopteran insects provides some of the most convincing quantitative tests of evolutionary theory.

In the final four chapters, we turn our attention to social behaviour. Under what circumstances would we expect the evolution of altruism, namely helping others to reproduce at the expense of one's own reproductive output? (Chapter 11). When would it pay individuals to cooperate with either related or unrelated individuals? (Chapter 12). We show how social theory can be tested in a variety of animals from microbes to meerkats. Chapter 12 is devoted to the social insects, where altruism reaches its most sophisticated development in the form of sterile worker castes. We discuss new theory for the genetic predispositions and ecological factors promoting this remarkable behaviour, and show that there are often conflicts of interest even within the most cooperative societies. In Chapter 14, we discuss how natural selection shapes signals, focussing on the evolution of honesty and deception.

Finally, in the last chapter (15) we return for a critical re-assessment of some of our main premises: the "gene's eye" view of behaviour, optimality models and evolutionarily stable strategies. We also point to the flourishing interactions with other fields of research.

The literature has become vast since the earlier editions of this book, so in this edition we have had to be even more selective. We hope that lecturers using this book will add their own favourite examples to those we have mentioned. Throughout, we have tried to point to gaps in current theory and evidence. We hope that readers will be inspired not only to fill these, but also to discover new problems to solve.