

The Evolution of Social Behaviour

How can the stunning diversity of social systems and behaviours seen in nature be explained? Drawing on social evolution theory, experimental evidence and studies conducted in the field, this book outlines the fundamental principles of social evolution underlying this phenomenal richness. To succeed in the competition for resources, organisms may either ‘race’ to be quicker than others, ‘fight’ for privileged access, or ‘share’ their efforts and gains. The authors show how the ecology and intrinsic attributes of organisms select for each of these strategies, and how a handful of straightforward concepts explain the evolution of successful decision rules in behavioural interactions, whether among members of the same or different species. With a broad focus ranging from microorganisms to humans, this is the first book to provide students and researchers with a comprehensive account of the evolution of sociality by natural selection.

Michael Taborsky is Professor of Behavioural Ecology at the University of Bern, Switzerland. His research focuses on evolutionary principles underlying social behaviour, combining empirical research on insects, spiders, fish, birds and mammals with theoretical and conceptual approaches.

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To our students, present, past and future

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Foreword

The fruitful interplay between social theory and field studies, which forms the central theme of this wonderful book, will be inspirational to new students and experienced researchers alike. Without theory, both to guide our observations and to interpret them, we ‘might as well go into a gravel-pit and count the pebbles’ wrote Charles Darwin in 1861 in a letter to a colleague. He was referring to geological studies, but his remarks, of course, apply with equal force to studies of social behaviour.

When I was a young student in the early 1970s, my bird watching was rescued from pebble counting by the ideas of David Lack, who had shown how an ecological stage of food resources and predation risk provides selection pressures which shape the evolution of avian social behaviour. I then remember my excitement, a few years later, when I first encountered Bill Hamilton’s theory of kin selection and the ideas of Robert Trivers and Geoff Parker on sexual and family conflicts.

Suddenly, a whole new world was opened up, one in which the stage for behavioural evolution was set not only by ecological pressures but by social pressures, too. At around the same time, DNA profiling became available as a method for precise measures of maternity and paternity in wild populations. This thrilling combination of new ideas and new techniques led to a blossoming of field studies of social behaviour, and discoveries of how individual decision making influences fitness, which have continued ever since and which are celebrated in this volume.

The tensions between social cooperation and conflict are familiar themes in our own lives and for centuries they have inspired our art and literature. Why, then, did it take so long to realize that these same tensions also seethe away in animal societies? Perhaps it was wariness of anthropomorphism; yet imagining what you yourself might do in a particular social situation, if you were a dungfly or a dunnoek, for example, is a powerful way of gaining insights into evolution because assessing the costs and benefits in order to choose the best course of action simulates the workings of natural selection.

The three authors here make a brilliant team. They have themselves made novel contributions to theory, but they have also all gone out into the field to test the ideas, with long-term studies of complex social systems: of cichlid fish in Lake Tanganyika (Michael Taborsky), of banded mongooses in Uganda and of paper wasps in Europe (Michael Cant) and of warblers in remote islands of the Seychelles (Jan Komdeur). Their painstaking field studies have shown the ingenuity needed to untangle how social behaviour influences fitness. All three parameters in Hamilton’s famous rule –

B, *C* and *r* – are challenging to measure and detailed observations and elegant experiments are needed to tease apart complex selection pressures. The two-way interaction between theoretical insights and field studies has revealed unsuspected richness in social behaviour in the natural world.

We are often warned how a peek at the ending before you start can spoil a book, but I recommend that this is exactly what the reader should do here. Start with the final box, a case study of our own species and how a careful consideration of kinship theory, evidence and comparison with another long-lived mammal, killer whales, gives new insights into the evolution of the menopause. Then work your way back to the front of the book through all the other boxes of the authors' case studies (ambrosia beetles, social cichlids, paper wasps, banded mongooses, Seychelles warblers). You'll then have experienced just the right mix of theory and respect for the complexities and wonders of the natural world to be ready to start at the beginning and to be inspired as you read the book right through.

Nick Davies
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Preface

The study of social behaviour is the most relatable of scientific topics, because all humans study social behaviour. Of course we spend a great deal of our time studying each other, but our fascination extends far beyond humans. As children we delight in poking insects or tadpoles to see what happens; later many of us become avid pet-watchers or naturalists. Our media wow us with stories about the curious lives of organisms we've never heard of, or new insights into the minds of the animals that we think we know best. All of us are captivated by wildlife films full of drama, struggle, and beauty. No doubt there are deep evolutionary reasons for our fascination with the behaviour of other organisms, and what they can tell us about ourselves. And, increasingly, we desire ultimate, evolutionary explanations of behaviour. It is no longer enough to describe what other organisms do. We want to know why.

This book is our attempt to explain why, or as much about why as we currently know. Behind the breathtaking film sequence or curious news story typically lies the quiet work of researchers and students who are, like us, fascinated by the why questions. We describe the evolutionary theories that attempt to explain why different patterns of social behaviour evolve and the evidence for or against these theories. Like any scientific subject, the study of social evolution is a Petri dish of evolution itself: a fierce competition of ideas, subject to fashions and fads, dissension and debate. An example is the group selection/kin selection debate, which has generated lots of heat *and* light. We've tried to concentrate on the light that is produced when brilliant ideas collide, and avoid where possible being drawn off course by whirlpools of debate.

We have two major foci that are evident throughout the book. The first is a focus on theory. The theory of social evolution has transformed our understanding of social behaviour over the last 60 years, and applies to every taxon of life. One of the most active frontiers of research is the social evolution of microbes, where experiments can follow the evolution of social behaviour over hundreds or thousands of generations in the laboratory. In the same university department one might find researchers using cultural evolution theory to understand the spread of human traditions and innovations over the last 10,000 years. The formal theories employed, rooted in population genetics and game theory, are the same whether the study system is a virus or a cancer, a slime mould or a human society, and whether information is inherited genetically or culturally or, increasingly, digitally. The reach of social evolution theory is remarkable, and provides an overarching framework for thought and

experiment on vastly different natural phenomena. This is one aspect of studying social behaviour that makes us feel fortunate in our choice of topic.

The second focus is on field research and reflects our own experience as behavioural ecologists who work primarily on wild animals. Field research is difficult to carry out and difficult to fund. It also has some powerful advantages. Studying natural populations gives us a picture of what variation is available to natural selection, and allows us to measure the fitness outcomes associated with this variation. Evolutionary models explore the evolution of adaptations, where an adaptive trait is that which has the highest fitness out of those traits that are available to natural selection. Fitness itself is a notoriously slippery concept to define, never mind measure, but field biologists have grown expert at measuring proxies of fitness such as the number of surviving offspring or, better still, lifetime reproductive success. In this way field research, particularly long-term research, can quantify the fitness consequences of alternative behaviour in animals living in the environment in which they evolved, exposed to their (coevolved) predators and pathogens, buffeted by unpredictable and uncontrolled ecological variation. The result is a line-of-sight connection between theory and the things being measured, and the chance to feed back lessons from reality, in all its messiness, into the neat and tidy models. Experiments under natural or semi-natural but controlled conditions can then nail down causal effects.

The book was motivated and organized by Michael Taborsky, who had the original concept and approached Jan and Mike to share the writing. Each section was spearheaded by one of the three authors, with lots of discussion and input from the other two. We completed much of the writing at a series of writing retreats in Switzerland, The Netherlands and the UK, where we could escape other responsibilities and talk at length in between putting pen to paper. Along the way we found many topics on which we had complementary expertise, but also different perspectives, gleaned from years spent watching and thinking about very different types of animal. Finding common ground by talking out our differences has been one of the most rewarding and interesting aspects of the work. Needless to say, we don't agree on everything, and we decided early on that the book was best served by allowing each of us to shape our parts of the text as we wished. So while we haven't tried to homogenize our voices, we've tried to find some kind of harmony between them, and to capitalize as much as possible on our varied experiences and study organisms.

This book aims to serve varied purposes. When thinking about fundamental concepts and the evidence for or against particular ideas, we had in mind our colleagues who would put our conclusions to the test. When outlining our framework and logic of thought, we tried to envisage how our information would help students to understand the evolutionary processes governing social behaviour. When indulging in our fascination for the staggering wealth of social patterns in nature, we thought of the interested amateur who might be prompted to take a closer look at behaviour and to make sense of the ecological circumstances that call forth one pattern rather than another. Above all, our hope is to transmit our enthusiasm for this topic to everyone who shares a curiosity and motivation to understand the sublime diversity of form and function in the world, and how we got here.

We are grateful to our universities for making this work possible and to Cambridge University Press for their patience and continued support, with a heartfelt thank you to our editors, Aleksandra Serocka, Jenny van der Meijden and Megan Keirnan. We acknowledge particularly our graphical designers, Michelle Gygax and Dick Visser, for their excellent illustrations, and Claudia Leiser for preparing the indices. We thank our colleagues Gerry Carter, Darren Croft, Raghavendra Gadagkar, Sjouke Kingma, Bram Kuijper, Nick Royle, Barbara Taborsky and Franjo Weissing for reading the book manuscript and helping us greatly to improve it. Last but not least, we owe thanks to our loved ones who generously condoned our occupation with this inspiring but time-draining endeavour.



The authors arriving at one of their writing retreats at a Swiss chalet.

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