Introduction
The uphill climb of sociobiology: towards a new synthesis

Tamás Székely, Allen J. Moore and Jan Komdeur

Social behaviour garners broad interest: biologists, social scientists, psychologists and economists all incorporate a consideration of social behaviour in their studies. This breadth of interest is unsurprising, as the vast majority of animals (and all that reproduce sexually) live partly (or fully) in social environments. As Robert Trivers (1985) succinctly put it, 'Everybody has a social life.' Some of this interest undoubtedly emerges because members of our own species (*Homo sapiens*) live in extensive societies and spend much time interacting with each other. Yet you do not have to be human for social behaviour to have a strong influence on biological processes. The significance of social behaviour is easy to see: if you isolate an ant, a fish or a bird from its peers in a sort of Kaspar Hauser setup, within a short time many of its 'normal' behaviours will change and be impaired. Social behaviour, heuristically defined as activities among members of the same species that have fitness consequences for both the focal individual and other individuals in the group, is thus ubiquitous.

The perplexing causes and far-reaching implications of social behaviour make it a rich subject to help understand evolution (Gardner & Foster 2008). The understanding of social evolution is challenging, given that social behaviour is often costly. Furthermore, unlike many traits that are passively selected by the environment, in the context of social behaviour the animals create selection for themselves by interacting with each other. This added complexity requires more complex models and clever experiments to disentangle cause and effect. Although the study of social behaviour goes back thousands of years (Dugatkin 1997), it is this complexity arising from interactions that fascinates evolutionary biologists.

Our enthusiasm for social behaviour led us to discuss the various ways we can study and understand social behaviour among animals. In 2006 the three of us drafted an outline of an ambitious book, and contacted Cambridge University Press with the outline. Our main motivation was the lack of a comprehensive volume that would cover both proximate and ultimate aspects of social behaviour, and go beyond taxon-specific treatises on some of the workhorses of social evolution (e.g. social insects, birds and mammals). Social behaviour has come a long way since the pioneering papers of Hamilton (1964) and Maynard Smith and Price (1973), and the landmark syntheses of Wilson (1975) and Trivers (1985). Given the stimulus of these papers and books, researchers investigated social behaviour with renewed vigour. Furthermore, the subsequent decades have applied new tools and new perspectives, and have gained new insights: advances in molecular genetics, neurobiology, mathematical theories of social behaviour and phylogenetic methods fundamentally changed the way we study animal behaviour, and what we know about social traits. We thought that to further advance sociobiology would require a comprehensive book which provides an overview of theoretical

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foundations and recent advances, and looks at implications beyond evolutionary biology.

E. O. Wilson (1975) defined sociobiology as a 'systematic study of the biological basis of all social behavior'. Sociobiology was created by population biologists and zoologists, and indeed Wilson wrote his tome as a true synthesis with the aim of pulling together theory and empirical data for (primarily) vertebrate social behaviour, having covered insect behaviour in an earlier book (Wilson 1971). For this reason, most scholars consider sociobiology sitting conveniently within the broad field of population biology. The agenda we set in this book, however, is broader and explicitly embraces genetics, developmental biology and physiology. We take Wilson's definition literally, and argue that investigation of any trait that has a bearing on social behaviour should justly be called *sociobiology*. Therefore, a developmental biologist who studies limb development may be labelled as a sociobiologist, if his/her objective is to understand how limb development and locomotion contributes to social traits – for instance, group foraging. Therefore, we view sociobiology as any aspect of evolutionary biology research that targets social traits.

Sociobiology is in the midst of a major paradigm shift. Early ethologists such as Konrad Lorenz, Niko Tinbergen, Karl von Frisch and their students provided a scientific basis of social behaviour by investigating group and family life, fighting, communication, display behaviours and mating. This ethological paradigm later split into studies of mechanisms (neuroethology, behavioural genetics) and function (behavioural ecology, sociobiology), as predicted by E. O. Wilson (1975). The two distinct approaches are now moving back towards each other. On the one hand, behavioural ecologists have begun to realise that functions cannot be fully understood without an appreciation of underlying mechanisms. For example, where traditionally behavioural ecologists studied how parents influence their offspring through nest attendance and feeding, modern researchers might investigate the same problem by considering the constituents of the egg in which the embryo developed, the architecture of the nest and how it influences physiological processes, and basic biochemical processes such as the role of antioxidants in offspring and parent fitness. Furthermore, there is an increasing interest in how these factors might interact and intersect.

On the other hand, geneticists, developmental behavioural biologists and neuroscientists are beginning to acknowledge that many of the genetic/genomic/neural processes may not make sense unless they are placed into an ecological context. There is a recognition that we need to understand the selective processes to which animals are subject in their natural environment. The most exciting studies of proximate influences on behaviour examine the interactions between the genome, development and the environment. We believe that investigating behaviour from this integrative perspective will lead our understanding of *eco-evo-devo*: the interplay between ecology, evolution, genes and development.

We have three major objectives with this book. Our first is to provide an overview of proximate and ultimate approaches to social behaviour. Social behaviour is all too often branded as a field dominated by behavioural ecologists, evolutionary psychologists and theoretical evolutionary biologists. We believe this perception is mistaken, because what makes social behaviour exciting is its fundamentally multidimensional nature. By contrasting examples from both mechanism and function, we anticipate that novel syntheses will emerge. For this reason, we have selected contributors who investigate organisms ranging from bacteria to humans, and who use a variety of research tools including a candidate gene approach, quantitative genetics, neuroendocrine studies, ecological studies of cost–benefit analyses, evolutionary game theory and phylogenetic analyses.

Our second objective is to produce an accessible overview of key topics in social behaviour for all students of behaviour, both academic and nonacademic. Social behaviour appeals to a broad audience in diverse biological fields and beyond biology: for instance, clinical scientists, psychiatrists and philosophers of science may find some chapters useful. Although the target audience for each chapter is undoubtedly the research field in which the authors work, we asked contributors to make their review broad. We hope that the book's accessible style will elicit cross-fertilisation between varied disciplines.

Finally, we also hope to inspire the new generation of students and young scientists. To fulfil this goal, we invited 21 guests to explain why they are interested in social behaviour. These guest profiles are short personal accounts from some of the most influential researchers in the field of social behaviour. Scientists are notorious for avoiding public attention; indeed, a major part of the scientific tradition is to remain objective, impersonal and neutral. However, this often hides extraordinary personalities, and conceals the persistence that drives many of us to study what we believe is interesting or important. The reader may find common themes among the elite of behaviour researchers. Those who have successfully altered how we view behaviour were often driven by pure curiosity. In an age where 'accountability' is increasingly used to mean 'applied' in research, it is refreshing to see that the main motivation for many researchers is a love of their subject, the organisms they study, or both.

When we embarked on this project, we were also hoping to establish common principles (or even a unifying theory) of social behaviour. We quickly realised, however, that our ambition could be only partially fulfilled (see Chapter 21). First, the field has expanded enormously since 1975, and each topic for which we envisaged one chapter would be more realistically covered by a whole book, or a set of books. Second, we had hoped to cover both proximate and ultimate aspects of social behaviour by soliciting contributors to tackle both. By and large we failed on the latter point, because in spite of promising (but often limited) interactions between researchers working on mechanistic *or* ultimate aspects of social behaviour, the field of social behaviour has remained divided due to the different scientific traditions and funding agencies. An alternative subtitle for our book could have been 'towards a new synthesis', because a synthesis, if achievable, is not yet complete.

We anticipate that the primary audience of this book will be graduate students, teachers, university lecturers and researchers. We envisage that the book will be suitable for graduate (or advanced undergraduate) discussions, and lecture courses in animal behaviour, behavioural ecology, evolutionary biology and psychology. The book is divided into three major parts: theoretical foundations (Part I), key themes (Part II) and implications (Part III). Chapters in Part I deal with modelling social behaviour from four perspectives (evolutionary genetics, game theory, phylogenetic inference and population genetics), and one chapter overviews how neuroendocrinologists investigate social traits. In Part II we selected some of the key themes in social-behaviour research (e.g. aggression, communication, group living, sexual behaviour, parental care and family life), and also invited contributions to dissect three pinnacles of social evolution: microorganisms, mammals and humans. Social insects are discussed in Chapter 6, and in profiles by Raghavendra Gadagkar, Bert Hölldobler, Laurent Keller, Gene Robinson and Edward O. Wilson. The main purpose of Part III is to look beyond these specific themes, and to investigate how sociobiology can be enriched by, and in turn can enrich, personality research, social cognition, population ecology, speciation and biodiversity conservation.

Having discussed various arrangements for the guest profiles, we decided to put these contributions in alphabetical order by name. We strongly recommend reading all of them: they are a testament to the diversity of approaches and personal philosophies that pervade some of the best research programmes. Most profiles are relevant to several chapters, and one chapter is often relevant to several profiles. The following chapters and profiles have the most obvious overlap: Chapter 1 (profiles by Keller, Queller, Robinson), 2 (Keller, Ritchie, Robinson), 3 (Haig, Robinson, Sherman), 4 (Haig, Milinski, Parker, Taborsky), 5 (Cockburn, Davies, Gadagkar, Hölldobler), 6 (Gadagkar, Queller, Taborsky, Trivers, Wilson, Zahavi), 7 (Gadagkar, Hölldobler, Hrdy), 8 (Hölldobler, Ritchie, Trivers, Zahavi), 9 (Milinski, Rainey, Sherman), 10 (Birkhead, Cockburn, Davies, Parker, Petrie), 11 (Birkhead, Davies, Parker, Petrie), 12 (Cockburn, Sherman, Taborsky, Zahavi), 13 (Queller, Rainey, Zahavi), 14 (Hrdy, Noë, Trivers), 15 (Hrdy, Noë, Wilson), 16 (Milinski, Noë, Petrie), 17 (Hrdy, Milinski, Trivers), 18 (Haig, Parker, Rainey), 19 (Birkhead, Keller, Queller, Ritchie), 20 (Cockburn, Milinski, Wilson).

This was an ambitious project, and we appreciate the enthusiasm expressed by our colleagues for such a book. A number of people supported the project right from its conception, in particular Amotz Zahavi, David Haig, Geoff Parker, Gene Robinson, Kevin Foster, Marla Sokolowski and Tim Birkhead, and we appreciate their continued encouragement. We further gratefully acknowledge the advice and comments of the following colleagues on book chapters and on profiles: Elizabeth Adkins-Regan, Suzanne H. Alonzo, Olaf Bininda-Edmonds, Bronwyn H. Bleakley, Russell Bonduriansky, Carlos A. Botero, Martha Brians, Charles R. Brown, Carel J. ten Cate, Andrew Cockburn, Patrizia D'Ettorre, Sasha Dall, Martin Daly, Anne Danielson-Francois, René van Dijk, Veronica Doerr, Jan Ekman, Gabriel Garcia-Pena, Patricia Adair Gowaty, Wolfgang Goymann, Kristine L. Grayson, Jim Groombridge, Elizabeth A. D. Hammock, Freya Harrison, Ben J. Hatchwell, Rebecca Kamila Hayward, Richard James, Laurent Keller, Bart Kempenaers, Min-Ho Kim, Clemens Küpper, Joel Levine, Erez Lieberman, Peter R. Long, Donna L. Maney, Manfred Milinski, Patricia J. Moore, Philip L. Munday, Ronald Noë, Ákos Pogány, Geoff Parker, John L. Quinn, Mike Ritchie, Stephan J. Schoech, Catherine E. Selbo, Andy Sih, Kevin M. Sinusas, Rhonda R. Snook, Nancy G. Solomon, Colleen Cassady St Clair, Áron Székely, Tamás Székely Jr, Gavin H. Thomas, Nina Wedell, Jonathan Wright and Gergely Zachar. Martin Griffiths, Abigail Jones, Hugh Brazier and Rachel Eley at Cambridge University Press provided unfailingly cheerful advice and help. The illustrations were kindly redrawn by Dick Visser, Groningen University. The stunning cover photo was provided by Alex Badyaev.

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Finally, we owe much gratitude to our parents, wives and children, who taught us first-hand the benefits, the significance (and sometimes the costs) of social environment.

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PROFILE

Undiminished passion

Tim Birkhead

My career in sperm competition has been a roller-coaster ride, energised by a number of particularly special moments. One occurred while I was studying guillemots *Uria aalge* on a group of uninhabited islands off the coast of Labrador in the early 1980s. Surrounded by sea-ice, magical auroras, humpback whales *Megaptera novaeangliae* and thousands of promiscuous birds, this was a wonderful study site. Plotting the results from my notebook at the end of one day, I became aware of what at that time seemed like a remarkable emerging pattern: extra-pair copulations were occurring exactly at the time in a female's cycle when they were most likely to result in fertilisation. It was one of those extraordinary moments when it was clear that everything was going to work out. Not only would this be (at that time) one of the most detailed studies of extra-pair behaviour in birds, it would also suggest that extra-pair copulations were adaptive (Birkhead *et al*. 1985). DNA fingerprinting was still a few years in the future, so it would be a while before we knew how this pattern would impact on fitness, but the behaviour was clear, and at the time my results seemed tremendously exciting. Importantly, they also raised many new questions. My obsession with seabirds, islands and sex, however, had started long before I went to the Arctic.

Like many of my generation of behavioural ecologists, I was a fanatical naturalist as child, encouraged by my father, a keen birdwatcher, and my mother, an accomplished artist. I was indulged – as a teenager I kept birds in my bedroom, whose walls (and carpet, inadvertently) I painted in my own designs. My mother fostered my enthusiasm and my father instilled in me two traits that today might seem old-fashioned: a strong work ethic and always to do my best. We lived in northern rural England, outside Leeds, and with a freedom almost unknown today I spent many days bird-watching alone or with friends. My life revolved around natural history: I raised young magpies *Pica pica*, rooks *Corvus frugilegus*, tawny owls *Strix aluco* and starlings *Sturnus vulgaris*. I collected insects and was the proud owner of an aviary of foreign birds. When I was 12 during a family holiday in north Wales I was taken by my father to Bardsey Island for the day. It was almost surreal in its perfection: thrift-covered cliffs, an azure sea and cerulean skies full of choughs *Pyrrhocorax pyrrhocorax*. As we walked across the island towards the end of the day we saw a young man sitting with a telescope and a notebook studying birds, and my father casually said to me, 'You could do something like that' – little realising how prophetic his comment was.

At school I was uninterested in (and therefore pretty useless at) everything except biology and art, frustrated at being imprisoned when I could have been outdoors. Maths, physics and chemistry were difficult because they were too abstract: I liked art and biology precisely because you could see them. I was

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encouraged and inspired by one or two extraordinary teachers – the combination of not finding all schoolwork easy, together with seeing how valuable good teaching could be, later made me aspire to be an effective teacher myself.

At about 17 I started to 'study' the grey heron *Ardea cinerea*, a species, like the peregrine *Falco peregrinus* and other raptors, whose numbers had been reduced by toxic chemicals. I knew I wanted to study herons, but with no guidance, I had no real idea of what to do. My 'studies' consisted of watching the birds at a daytime winter roost near Farnley Park, a beautiful estate where 150 years previously J. M. W. Turner had painted landscapes, herons and other birds. I spent entire winter days huddled in the undergrowth watching these majestic birds, elated by the occasional flurry of raised plumes as birds disputed the best roost location. If nothing else, my heron-watching honed my observational skills and powers of endurance.

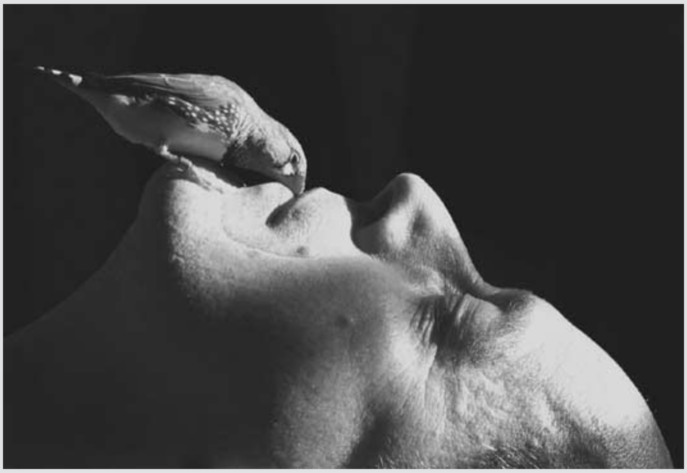
I went to Newcastle University to read zoology in 1969 and loved it. My most inspiring teacher there was Robin Baker, who told us about the then unpublished work of Geoff Parker and Bob Trivers on sperm competition and sexual selection. Hearing about this and seeing the logic of individual selection for the first time was an extraordinary moment. I was inspired, and decided there and then that I would pursue the study of sperm competition in birds.

During one university vacation I worked on a relative's farm in Cornwall. Knowing of my interest in herons, he told me that an old school friend of his, Ian Prestt, was investigating the effect of pesticides on herons and other birds at Monks Wood Experimental Station. A letter secured me an invitation to experience this research first hand, and before I knew it I had the keys of a Land Rover and was allowed to study the herons' social behaviour on my own. It was exhilarating. I felt I was doing something constructive, and it was great to be able to come back each day and enthuse about what I had seen. At Monks Wood I met John Parslow, who later offered me a vacation job looking at guillemots on Skomer Island, Wales. John was also interested in the effects of toxic chemicals on seabirds, and found an excuse for me to go to Skomer.

Before that, I attended the Edward Grey Institute student conference in Oxford in the spring of 1972. David Lack was director of the EGI, and he asked the gathered group of students if anyone was interested in undertaking a DPhil. He preferred to walk rather than sit, so my 'interview' took place walking up and down outside St Hugh's College in light rain. I babbled on about my interest in individual selection, social behaviour and sperm competition, and Lack, who didn't say much, merely commented that he knew more about ecology than behaviour. By the time I returned to Newcastle I had an offer. With no further discussion, Lack presumed that I would study guillemots on Skomer, since that was what I was going to do for John Parslow as soon as I graduated. With hindsight, I realise that Parslow and Lack had colluded – luckily for me.

The guillemot was a fortuitous choice. Although I was interested in sperm competition I had no idea when I started my DPhil. that the guillemot, despite being socially monogamous, was sexually rather promiscuous. The observations I made were promising, but I soon realised that without a large number of individually marked birds in close proximity, guillemots would take me only so far in sperm competition. On moving to Sheffield in 1976 I started what would become a 10-year study of magpies to look at mate-guarding and extra-pair behaviour. But I was still in love with seabirds, and I spent the next seven summers in various parts of the Canadian Arctic. Labrador, however, was the tipping point. The colonies there provided exactly the opportunity I needed to follow the behaviour of individually recognisable guillemots. As all the pieces started to fit together, I made the decision in the spring of 1983 that from then on sperm competition would be the main focus of my research.

Social behaviour was only part of the story. A true understanding of sperm competition also required a proper understanding of the mechanistic aspects of reproduction: how sperm were utilised, where and



Tim Birkhead and zebra finch. Photo: Francesca Birkhead.

when fertilisation occurred, and so on. Capitalising on avicultural skills acquired as a teenager, I made the zebra finch *Taeniopygia guttata* one of the two model species I would study (Birkhead 1996).

The second was a serendipitous choice – the fowl *Gallus gallus*. In the late 1980s I was invited to a meeting at the University of Stockholm's field station at Tovetorp in southern Sweden. During a tour of the facilities we were shown enclosures containing lynx *Lynx lynx*, moose *Alces alces* and other macho large mammals, all of which were being studied by rather macho research students. Suddenly a group of feral fowl (a primitive domestic fowl very similar to the red jungle fowl) scuttled past us and a male forced a copulation almost at our feet. Taken aback, I asked my host which of the various research students was studying these birds. Slightly incredulous, he said 'no one' – they were simply 'decoration'. I was intrigued, and a year or two later Tom Pizzari (see Chapter 10) was there as my PhD student studying their behaviour. I had mentioned to Tom that if he could persuade the cockerels to copulate with a stuffed female we might be able to obtain natural ejaculates, as I had done with zebra finches, and thereby gain new insights into both their copulation behaviour and the mechanics of sperm competition. It seems surprising that after decades of poultry research, no one knew how many sperm a male transferred during copulation. Despite his best efforts, Tom was unable to persuade the males to perform with his stuffed female. I went out to Sweden and one afternoon, as we watched the birds together, Tom was called away to the phone. In his absence I caught a live female (they were habituated and extremely docile) and, placing her feet between my fingers, crawled on my belly, with her rear end facing away from me, towards a cockerel. Slightly incredulous at his good fortune, the male mounted and inseminated the female. I let her go and tried another female. It worked again. I knew then that we were on the threshold of something exciting. Tom returned from his phone call, and I said to him, 'Watch this.' Once again the birds performed. Within a matter of hours we had devised a way of collecting ejaculates from the female, allowing us to measure ejaculate size and opening up a rich new avenue of research (Pizzari & Birkhead 2000, Pizzari *et al.* 2003).

What has guided my research? (1) First and foremost, a ceaseless intellectual curiosity about the natural world. The freedom I had as a youth to spend countless hours watching birds and other animals honed my field skills, fuelled my fascination for biology and gave me a strong sense of what I call biological intuition. That is, recognising what is biologically meaningful, what is likely to work and what isn't. (2) Enthusiasm. I'm not sure where enthusiasm comes from, but my zeal was fostered and encouraged by my parents, and it has continued to provide the drive and tenacity that research requires. (3) Excellent teachers and wonderful colleagues. The Edward Grey Institute provided a particularly stimulating, challenging and instructive environment when I was a DPhil. student. Subsequently I have been extraordinarily fortunate to have had a succession of outstandingly able research students and other colleagues to keep me on my toes. (4) Open-mindedness. By this I mean reading and interacting widely (not just within behavioural ecology), and embracing broad horizons. There is no better way of generating new ideas than looking beyond the boundaries of one's own discipline (Birkhead 2008).

Finally, the best thing of all about being a behavioural ecologist is that one's enthusiasm for the natural world actually increases over time. The more we discover, the more we discover that there is still more to discover. Even after 40 years in the business, my passion for birds and for biology in general is even greater than when I started.

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PART I

Foundations

1

Nature–nurture interactions

Marla B. Sokolowski and Joel D. Levine

Overview

Inheritance is associated with a paradox: it roars with the survival of the species, while at the same time it whispers a fragile message that is constantly modified even among kin. The genes, the environmental context and the traits that arise from their interaction are interrelated. A complexity that characterises this three-way relationship has been attributed to the nature–nurture dichotomy. Traditionally, *nature* is understood to mean *the genes*, whereas *nurture* denotes *the environment*. So, for example, people may debate why one pumpkin is superior to another – was it the quality of the soil or other growth conditions in the pumpkin patch, or was it the specific combination of alleles in that pumpkin's genome?

In recent years, there has been a long-overdue paradigm shift from a limited focus on the nature–nurture dichotomy to a more expansive view that includes gene by environment (G × E) interactions and even gene–environment (G ↔ E) interdependencies, as defined and discussed in this chapter (Rutter 2007). A mechanistic basis for the concept of interdependency arose from advances in molecular biology and genomics which show that DNA is not only inherited but is also environmentally responsive. The latter argument is supported by findings that individuals with dissimilarities in their DNA (DNA polymorphisms) are differentially affected by the same environment. Different environments through development and adulthood can affect individuals with one genetic variant but not another. Individuals, by virtue of their genetic variants, may prefer certain environments, and, in turn, the experiences they acquire in a chosen environment affect the expression of their genes. And finally, the DNA of individuals with the same genetic variants is differentially modified by experience, and this modification is inherited. Studies of gene–environment interdependencies in social behaviour are tremendously challenging. The environmental term is necessarily multifaceted and laced with abiotic and biotic factors that vary in time and space. However, the developing union between this conceptual framework and the new tools in genetics, molecular biology, genomics, animal tracking and imaging greatly facilitates these studies.

In this chapter we address the paradigm shift from (a) nature–nurture to (b) G × E and onwards to (c) G ↔ E interdependencies, with an emphasis on social behaviour. We first approach this shift from a historical perspective, and then move on to discuss experimental designs, behavioural plasticity,

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