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## Introduction

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Some of the most conspicuous behaviours performed by an animal are related to communication – communication that mediates reproduction and survival. As explained below, a knowledge of animal communication is important in more respects than simply its role in understanding such fundamental aspects of animals' lives. This book is about a perspective that can increase our understanding of animal communication.

One way in which animal communication is important is that it interfaces with and links several fields of study. In the field of behaviour, for example, communication is often used to illustrate Niko Tinbergen's four types of question (function, mechanism, development and evolution) and how the answers complement each other (e.g. Krebs & Davies, 1993). Communication has interfaces with many other areas of biology including evolution, ecology, population genetics, neurobiology and physiology. For example, it can be a window into the cognitive worlds of animals (e.g. Ch. 24). Links with other sciences are shown by the use of ideas and techniques from psychology to understand how communication is perceived (Ch. 20), and using information from physics and chemistry to explain how communication is achieved (e.g. Bradbury & Vehrencamp, 1998).

Communication cannot occur in isolation; it is an inherently social behaviour. This makes it even more surprising that the wider social context in which communication takes place is rarely considered explicitly. As explained in the next paragraph, it is likely that communication commonly occurs in the context of a network of several animals. This chapter is both a brief introduction to this context – animal communication networks – and an explanation of this book's structure.

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**About communication networks**

A communication network is a group of several animals within signalling and receiving range of each other. If signals travel further than the average spacing between individuals, then there is potential for a communication network to exist. This is as true for the ocean-spanning songs of whales as it is for the begging calls of songbird nestlings crammed into a nest cavity, and it is why networks can be considered to be the commonest context in which communication occurs (e.g. McGregor & Peake, 2000).

This would seem to be stating the obvious, especially to those new to the field of animal communication. Indeed, those studying chorusing animals, particularly insects and anuran amphibians, have long adopted a network perspective and recognized the importance of doing so (e.g. Otte, 1974). However, it is only relatively recently that other types of communication have been considered explicitly in a network context. Communication was, and still is in many instances, treated as occurring between two individuals – the signaller–receiver dyad – perhaps because this is the simplest relationship possible between the three basic components found in communication (the signaller, the signal and the receiver). In this sense, a dyadic view of communication follows from the stricture of Occam’s razor (also known as the law of parsimony) to employ the simplest explanation consistent with the facts. While agreeing wholeheartedly with this standard scientific practice, it is clear that a dyadic view of communication is often not consistent with the facts. One example is the high signal level used in close-range aggressive encounters – human antagonists nose to nose, yet shouting at each other – surely high signal levels are not needed to achieve signalling at such close range? In a network context, such high levels make more sense, because there may be more distant intended receivers (the gathering crowd in the human example) in addition to the opponent (Zahavi, 1979). Many further examples of communication that are best considered in the context of a communication network are found throughout this book.

Another reason for explicitly considering communication in a network context is that it identifies communication behaviours that cannot occur in a dyad. A good example is eavesdropping, particularly social eavesdropping (Ch. 2) in which the eavesdropper extracts information from a signalling interaction between others. Social eavesdropping requires a minimum of three individuals (one eavesdropping, two more interacting) and, therefore, falls outside a dyadic view of communication. The evidence for eavesdropping and its wider implications (e.g. for comparative cognition) is presented in many of the chapters of this book. Eavesdropping and similar network behaviours discussed in this book are considered by many to be a compelling reason to adopt a network perspective.

*Communication networks and eavesdropping*

It is perhaps worth emphasizing that, while eavesdropping is a good example of communication network behaviour, it is not the only one, and the value of the communication network perspective does not depend on a demonstration of eavesdropping. The reason for its current prominence is that it was considered first and, therefore, at the moment it is more prevalent in the literature. There is no merit in shoe-horning a natural example into a definition of eavesdropping, nor in judging the value of any natural communication behaviour by how well it fits this (or any other) definition. As several chapters demonstrate (e.g. Chs. 9 and 23), such examples from the real world can probe and challenge our definitions (e.g. of interactions and of communication more generally) and the thinking that follows from them. The result can be considerable insight and lead to progress for the whole field of communication.

**A note on definitions**

Clear and workable definitions are the essential basis for meaningful discussion. I have tried to ensure that terms are used clearly and consistently within a chapter, but there may be good reasons why chapters differ in the detail of their definitions (e.g. for reasons discussed in the previous paragraph). There are no instances in this book where the same term is used in a markedly different way in different chapters, but readers should bear in mind that the detail of the definition may be important to the topics discussed by the chapter.

There are two nice illustrations of the problems that definitions can create. The first concerns eavesdropping. Alan Grafen pointed out a problem with the term eavesdropping after I had used it when presenting ideas on communication networks at the *Royal Society Meeting on Signalling* in 1992 (McGregor, 1993). The problem he foresaw was that in everyday use the term means secret information gathering, and it was clear to him that there may be advantages to the signallers in providing information (i.e. promoting eavesdropping), especially if the signaller had won the agonistic contest (see also Zahavi, 1979). The everyday meaning of eavesdropping and its implicit association with acoustic signals have been at the root of several misunderstandings that could perhaps have been avoided if a more neutral term had been used (at the time Grafen suggested type II receivers). Tom Peake has sorted out this and other problems to do with definitions of eavesdropping with admirable clarity in Ch. 2. Nevertheless, information gathered without the source's knowledge may have particular value, as John Locke discusses in Ch. 19. I think this demonstrates that identifying the secrecy or otherwise of information gathering is the route to progress, rather than rigidly applying a definition.

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The second example concerns the relationship between information and communication. In my view, the terms are clearly not synonymous; rather signals are a subset of information because they are specialized to transmit information (more details in McGregor & Peake (2000)). This could have created a problem with semiochemicals: if they are not signals (i.e. they contain information but are not specialized to transmit it) then the behaviour involving them is not communication and the concept of communication networks would not apply. Fortunately for the book, Brian Wisenden and Norm Stacey thought carefully about the issue and realised that there were many important similarities that gave them an opportunity to discuss the functional and evolutionary relationships between information, signals and networks (Ch. 23). So a problem arising from definitions has given real insight, rather than the acrimonious defence of definitions that is all too common in the literature.

### About this book

#### *Coverage*

There are several types of book on animal communication. Some are synoptic treatments of the whole topic (e.g. Hauser, 1996; Bradbury & Vehrencamp, 1998) whereas others concentrate on particular types of signal such as pheromones (Wyatt, 2003) or on a group of animals such as arthropods (Greenfield, 2002). Many books do both, for example dealing with acoustic communication in insects (Gerhardt & Huber, 2002) or birds (Kroodsma & Miller, 1996). This book is rather different in that it looks at a specific topic in communication and covers several modalities and taxonomic groups.

#### *Organization*

Each chapter has been written so that it can be read alone, since this is a common way for edited volumes to be read. Inevitably, this has led to some similarity between chapters in their opening remarks, but I think this is more than offset by each chapter having its own reference section. The many cross-references to other chapters in the book also show the extent to which authors have taken account of material in other chapters and made links between them.

A second way in which the book has been given overall coherence is to group the chapters into four parts that reflect major aspects of communication networks. Each of these parts is prefaced by a short overview that identifies chapter themes and highlights some of the issues that remain to be tackled. The fact that many chapters could have been put into any of the four parts further demonstrates the extent of overall coherence of the book and the wide-ranging nature of the

chapters. Within each part, there is no particular order of chapters, although in Part III the order is loosely phylogenetic.

The chapters grouped into Part I deal with communication behaviours, such as eavesdropping and audience effects, that involve three or more individuals (i.e. a communication network) and as such fall outside the 'classical' or traditional dyadic (one signaller and one receiver) approach to communication.

Part II groups particular contexts that are fruitful to consider from a communication network perspective: mate choice, predation, begging, aggression and scent marking.

The reason for grouping chapters in Part III is taxonomic: from fiddler crabs to humans via most groups of vertebrate. While communication networks may be more or less ubiquitous, features of different taxa (e.g. main senses, social organization) can have a major effect on the details of communication networks and provide insight into the topic as a whole.

The final part contains chapters that, to a greater or lesser degree, link communication and other disciplines in biology and more widely in science. From the evidence of these chapters, a network perspective seems to be particularly valuable at such subject interfaces.

### Summary

There are several reasons for considering that the natural context in which communication occurs (and in which it has evolved) is a network of several animals in signalling and receiving range of each other. However, this context has not been considered explicitly in many studies of animal communication. The chapters in this book apply a communication network perspective to a variety of taxa using a number of signal modalities in several circumstances. The results are illuminating. To modify a marketing phrase used for mobile phones: the future is bright; the future is a network view of communication.

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Part I BEHAVIOURS SPECIFIC TO  
COMMUNICATION NETWORKS

## Introduction

The reason for grouping together the chapters that appear in this part of the book is that each of them concerns communication behaviours that are best viewed from a communication network perspective, rather than from the more common dyadic (one signaller to one receiver) standpoint. It is a fact that, with the exception of choruses, most studies to date have implicitly or explicitly considered communication between a dyad. Although the communication network perspective of several signalling and receiving individuals seems to follow logically from what we know of natural communication, the dyadic viewpoint has historical precedence and considerable inertia. A network perspective will become more commonly adopted only if it is clearly better able to explain communication behaviours than a dyadic approach. It is for this reason that a network perspective has long been adopted in studies of choruses; the effect on an individual's signal timing of the signals of nearby conspecifics can be striking patterns, such as signal synchrony in the chorus (e.g. Greenfield, 2002; Ch. 13). Such patterns cannot be explained by considering communication as a dyad. All of the chapters in this book demonstrate the value of adopting a network perspective; however, it gives this demonstration more emphasis to begin with a section covering communication behaviours that are particularly suited to, or associated with, a network perspective.

### Eavesdropping

In Ch. 1, eavesdropping is identified as a receiving behaviour that has been particularly identified with, and is only possible in, a communication network. The first two chapters of Part I look at eavesdropping in more detail.



## 10 Part I

In Ch. 2, Tom Peake summarizes the evidence for eavesdropping in different contexts and also discusses the diverse use of the term in the literature. His division of eavesdropping into interceptive eavesdropping (e.g. predators locating prey from prey signals) and social eavesdropping (extracting information from a signalling interaction) is an important clarification. However, as Tom points out, clarifying definitions is more important as means of moving arguments on from the question of whether a given behaviour can be called eavesdropping or not and towards a more fruitful and general approach based on the nature of information transfer.

Torben Dabelsteen deals mainly with social eavesdropping on the acoustic signals of birds in Ch. 3. He identifies the potential costs and benefits of eavesdropping and uses information from studies of how bird song transmits through the habitat to explore how eavesdropping is best achieved. The overall balance of costs and benefits of being eavesdropped upon will determine whether signallers promote eavesdropping on their signals or whether they try to avoid it. One intriguing possibility that Torben discusses is whether the costs of being eavesdropped upon could be avoided if signallers made their signals anonymous by removing information on signaller identity.

### Audience effects

In communication networks, several receivers are likely to be present during signalling interactions between others; these receivers do not take part in the interaction and have been referred to as an audience. The effects they can have on signalling behaviour are the subject of Ch. 4, in which Ricardo Matos and Ingo Schlupp draw the distinction between an apparent audience and an evolutionary audience. The distinction is important because selection pressures imposed by the presence of audiences in the evolutionary past of the animals may result in features of the signalling interactions despite the absence of an audience during any particular interaction. Also, whether an audience is apparent to the signallers involved in interactions may depend on signal modality: individuals have to be in the line of sight of visual signals to receive them and, therefore, an audience is likely to be apparent; however, the same is not true of widely broadcast acoustic signals.

### Bystanders

Being a bystander (i.e. present, but not directly involved) during an agonistic or mating interaction can affect subsequent aggressive and mating behaviour and is explored in Ch. 5. Ryan Earley and Lee Dugatkin focus on social eavesdropping (a subset of bystanding) by two species of poeciliid fishes that are likely

to be familiar to many – green swordtails *Xiphophorus helleri* and guppies *Poecilia reticulata* – and that communicate largely with visual signals. Their chapter shows how a network view can encompass and organize diverse aspects of fighting and mating behaviour (including mate copying); it also identifies the many conditions that favour eavesdroppers and how the effects of eavesdropping are manifested.

### Victory displays

In the final chapter of this section, John Bower examines victory displays: signals produced by the winner (but not the loser) after an aggressive interaction. There has been surprisingly little work specifically on this topic, despite the wealth of studies of signalling before and during aggressive displays, and such information is widely scattered. Chapter 6 collates the information on victory displays and then interprets its functional significance, first from a dyadic perspective and then from a network perspective. It may have been premature to include victory displays in this section, because on current evidence it is not clear that victory displays always function in a network context rather than in the winner–loser dyad. However, even if their main function is dyadic, their conspicuous nature makes it likely that other individuals could gain useful information by paying attention to victory displays.

### Future directions

The authors dealing with eavesdropping make several suggestions for the directions future research should take: incorporating eavesdropping into theoretical models to derive testable predictions that can contribute to understanding signal evolution (Ch. 2); finding evidence of eavesdropping in non-experimental natural contexts (perhaps by using a combination of tracking and acoustic location technologies to follow the individuals in a network), and continuing such studies long enough to identify differences in reproductive success (Ch. 3); unravelling the complex interrelationships between features of individuals, their social and wider environment and the role of bystanders in order to understand communication fully (Ch. 5).

The authors dealing with eavesdropping clearly consider that the phenomenon is now well characterized. In contrast, victory displays clearly need more detailed study in order to establish the phenomenon and to elucidate its function and whether it is network phenomenon. It is likely that controlled laboratory experiments are the best way to investigate what effect, if any, victory displays have on other members of the communication network (Ch. 6).

Progress in understanding audience effects seems likely to come from a different type of approach. In addition to modelling and controlled experiments, there is