Part I

Introduction to primate communication

1 What is primate communication?

This chapter starts with a general introduction to the two main components of this book: primates and communication. After describing how the term communication is used in this book and how communication can be approached on different levels, primates are introduced with a focus on the variety of their social systems and potential factors that influence their formation. Finally, this diversity of primate social systems is discussed with special reference to the role of communication in maintaining such complex social systems. However, while the aim of this chapter is to provide an overview of primates and their communication in different social systems, Chapter 10 will focus in more detail on the evolution of primate communication with special reference to the role of social organization in the emergence of particular communicative systems.

1.1 What is communication?

Scientists are often particularly interested in the communication of primates, as opposed to other animals, in the hope that it will shed light on the evolution of human communication. The assumption underlying this comparative approach is that as monkeys and apes are phylogenetically closely related to humans, both human and nonhuman primates must share characteristics in the way they communicate. One specific hope, of course, is that an understanding of primate communication will lead to a better understanding of the evolution of human language.

Human communication (especially language) involves various complex (and perhaps evolutionarily recent) cognitive processes. A comparative approach searching for the precursors of human communication in other primates, therefore, often targets these processes for comparison. As such, the study of primate communication can be driven in a slightly different direction to the study of other animal communication, where such cognitive processes are not looked for. It is important that this theoretical and methodological bias is acknowledged in order to make true comparisons between primate species and other animals. We can attempt to untangle this problem by going back to basics and considering precisely what communication *means*, and how we can study it in different ways. There is much debate over how to conceptualize animal communication, however, and scientists are often criticized for overusing language metaphors (**Box 1.1**). In the following section, different approaches to communication will be discussed, and then communication will be defined for the purpose of this book.

Box 1.1 Do researchers rely too heavily on language metaphors to conceptualize animal communication?

Many researchers study animals with the goal of trying to understand the phylogenetic history of human linguistic abilities (see Chapter 5 and 10), and consequently animal communication research has been heavily shaped by terms and concepts from the study of human language. Rendall, Owren, and Ryan (2009) recently reignited the debate about the utility of such an approach and heavily criticized the use of linguistic terms in animal communication research. They argue that casual and inconsistent use of terms such as 'information' and 'meaning' lead to unnecessary confusion and facilitate inappropriate conceptualization of communication. In particular, the use of such terms encourages researchers to rely (consciously or not) on Shannon's (1948) intuitively appealing *Theory of Information*. This theory, originally conceived in an engineering context to describe the effective reproduction of a symbol across noisy physical channels, involves the signaller encoding and transmitting information for subsequent decoding by the receiver. Rendall, Owren and Ryan (2009) argue, however, that such a system can only apply when there is parity between the signaller and receiver in terms of common representational processes to allow accurate encoding and decoding of the information in the signal. Thus the signal has to be represented by the sender and the receiver in the same way. It is clear, however, that many communicating animals may not be capable of sharing such representations and that the goals and processes of signallers and receivers may not be the same (Rendall, Owren and Ryan, 2009). As such this conceptual framework is argued to be inappropriate for animal communication and some would also suggest human language (e.g. Scott-Philips, 2010).

As an alternative framework, Rendall and colleagues (2009) and Scott-Philips (2010) advocate thinking of communication in terms of influencing others, not informing them. This builds on seminal arguments proposed by Dawkins and Krebs (1978), who suggest that signallers primarily produce signals to manipulate receivers. Other researchers see more utility in preserving the concept of 'information' in animal signals (Seyfarth *et al.*, 2010) and deny that the use of terminology such as 'information transfer' necessitates reliance on language metaphors and Shannon's *Theory of Information*. Seyfarth and colleagues clarify that information can be usefully defined as reducing uncertainty in the receiver, allowing them to predict current or forthcoming events. Font and Carazo (2010) attempt to unify these 'information' and 'influence' camps with a view of communication where signallers influence receiver behaviour in ways that increase their fitness and receivers 'eavesdrop', extracting information from signals that the signaller may not intend to have provided them with. Interestingly, this is not dissimilar to traditional views of animal communication within ethology.

Whilst it is undoubtedly the case that the pursuit of understanding the information available to and extracted by receivers from animal signals has positively advanced our understanding of animal communication in a number of ways (Seyfarth *et al.*, 2010), the search for consensus on a more appropriate conceptual framework in which to embed animal communication research is ongoing.

In **behavioural ecology**, communication has been defined as 'the process in which actors use specially designed signals or displays to modify the behaviour of reactors' (Krebs and Davies, 1993, p. 349). The phrase *specially designed* is crucial, as it qualifies that the signals or displays must have been selected via evolutionary processes, specifically for the purpose of communication. Importantly, such signals should be decoded by the receiver successfully (Burling, 2005), otherwise they would not evolve. There could be many *cues* that indicate something to a conspecific, and which can be used by the conspecific to alter their behaviour, but unless this has been shaped by evolution to form a specific adaptation, it would not count under this definition. For example, two monkeys sit facing each other, grooming. One monkey sees a conspecific join the group, and shifts her eyes to watch this new individual. The monkey grooming her observes this eye movement, and follows her gaze. Information about the incoming individual is shared through this process, but does this count as communication? A behavioural ecology perspective would argue that this is not communication, but instead that the eye movement functioned as a cue to information (for the receiver). Aspects of this process could, however, be acted on through evolution and become fixed as communicative signals or displays. Eye movements could, for example, become more salient through adaptive change in the morphology of the eyeball and the coloration of the sclera, and thus gain signal function (Kobayashi and Kohshima, 2001). Interestingly, white **sclera** is only typical for humans, possibly having evolved as a specific adaptation for cooperative communication (Emery, 2000) (see also Chapter 2, section 2.3.1).

Another distinction divides communication into that which involves behaviour, and that which does not. In his classic work *The Behaviour of Communicating*, the ethologist W. J. Smith defines communication as 'the behaviour that enables the sharing of information between interacting individuals as they respond to each other' (Smith, 1977, p. 2). Importantly, this definition excludes static and invariant displays, such as the brightly coloured wing of a butterfly or the peacock's tail. Of course, the line might be blurred in many cases, as the salience of a static signal can be increased through behaviour. The dance of the male stickleback, for example, is paired with his red colouration in the mating season. The distinction between behavioural and non-behavioural communication, however, is a useful one in order to narrow the focus of study, and one that is adopted throughout this book. As such, although there is a vast range of fascinating and important primate signals, they will not be considered here unless explicitly related to behaviour. Thus, the facial colouration of the mandrill, the sexual swellings of female crested macaques and the striped tails of ring-tailed lemurs, for example, are not considered further within this book.

One aspect of communication that has not featured in the previous definitions, and yet is a feature that is central to the interest to many scientists, is that of intention. For the aforementioned Krebs and Davies (1993), Smith (1977) and many other scientists with a more biological leaning, the issue of proximate *motivation* on the part of the sender is largely irrelevant. The role that the communication plays in the social interaction, and how this has been shaped by evolution, is their primary concern. For scientists with a more psychological perspective, in contrast, whether or not the communicative events are **intentional** is a key question. Primarily, this stems from the goal to shed light on the evolution of human communication (and language in particular) through studying

primates. As much of human communication is intentional, many psychologists are interested in whether primate communication is also intentional, and thus may have been an important precursor to language. Thus, Tomasello (2008, p. 14) uses a narrower definition, and defines communicative signals as 'signals that are chosen and produced by individual organisms flexibly and strategically for particular social goals, adjusted in various ways for particular circumstances. These signals are *intentional* in the sense that the individual controls their use flexibly towards the goal of influencing others.' Note that Tomasello (2008, p. 14) distinguishes *signals* from *displays*, and refers to displays as 'prototypically physical characteristics that in some way affect the behaviour of others', which are 'created and controlled by evolutionary processes', which seems to indicate that the sender has no voluntary control over their production. Determining whether a signal is intentional and voluntary is not straightforward, however, and so the issue of intentionality and how this relates to communication will be discussed in more depth in Chapter 8.

For the purpose of this book, communication is defined as *social behaviours that transmit information from one individual to another*. How these behaviours can be identified is, of course, part of the challenge and process of study. Throughout this book, we refer to four different modes of primate communication that have (historically) been studied separately: gesture, facial expression, vocalization and olfaction (see Chapter 4 for a more detailed discussion of this categorization). Our aim is to argue that these modes should be studied simultaneously and (where possible) using similar methods in a multimodal approach (see Chapter 5 for a discussion on how to define multimodality).

1.1.1 Understanding communication at different levels

The distinction between psychologists and biologists is always hazy within the study of animal behaviour, as the topic necessarily sits on the cusp of these two disciplines. There are times, however, when it is helpful to understand the difference between these two parent disciplines in order to unpack the nuances between differing approaches. Historically, psychologists have been more interested in the mechanistic aspects of behaviour (the immediate, causal processes), whereas biologists have focused more on the functional aspects (why/how that behaviour has evolved). One reason that scientists use different definitions for communication is that they are looking at communication from these two different perspectives, which can boil down to a focus on the **proximate** level, or a focus on the **ultimate** level.

In 1963, Niko Tinbergen was well aware of the divisions that existed between scientists interested in behaviour, and following on from Mayr (1961) endeavoured to unify the field in his landmark paper 'On aims and methods in ethology' (Tinbergen, 1963). His main aim was to highlight that there are four different but related levels at which behaviour operates and thus can be studied, but that a focus on each level makes a valuable and necessary contribution to the study of behaviour. Importantly, he emphasized that all levels share a common goal – to understand behaviour. Often called Tinbergen's four questions, or *four whys*, he described these four levels and in doing so, he constructed a framework for the study of behaviour which has offered clarity ever since. **Box 1.2** shows a unit of communication (a facial expression), and outlines how this could

Box 1.2 Analysing signals at Tinbergen's four different levels: 'why' is that primate showing a 'playface'? (Photo: Jérôme Micheletta)

Level of explanation		Example: 'Playface' of crested macaques
Proximate: *How* an organism works (focus on individuals)	Causal/ Mechanistic	Psychological (e.g. cognitive, emotional) and physiological processes underlying the behaviour: *He is feeling playful, the facial muscles are activated by the corresponding neural substrates and the facial nerve.*
	Developmental/ Ontogenetic	Developmental processes that have led to the production of the behaviour: *He started producing the 'playface' during playful encounters from birth, possibly due to innate processes, and its use may have been refined through experience.*
Ultimate: *Why* an organism works like that (focus on species)	Phylogenetic/ Historical	The history of the behaviour over evolutionary time: *Crested macaques inherited the behaviour from ancestral primate species, which used a similar facial expression during play.*
	Functional/ Evolutionary	The adaptive function of the behaviour for the species: *Communicating motivation to play is adaptive as it helps coordinate and maintain play bouts, which is a useful social behaviour.*

be explained at the four different levels. First, Tinbergen described *causation*. This relates to the 'preceding events, which can be shown to contribute to the occurrence of the behaviour' (Tinbergen, 1963, p. 418). Specifically, this relates to the mechanism associated with the behaviour, the physiology and the cognitive and emotional experience. Second, Tinbergen described *survival value*. Here, the function of the behaviour is considered in

terms of why it has been selected by evolution, and how it is adaptive. What survival value does the behaviour offer? What is it good for? Third, Tinbergen described *ontogeny*. Ontogeny relates to the development of an individual during its lifetime. Of particular interest are how different variables influence the manifestation of certain behaviours, and the extent to which behaviours can be modified or are present from birth. Fourth, Tinbergen described *evolution*. Often confused with survival value, this level does not directly consider adaptation, but instead the phylogenetic history and relationships that exist between **extant** and extinct species that reflect evolutionary ancestry. Here, it is the evolutionary path of an organism that is of interest, not necessarily the selection pressures that directed that path, or the solutions to the problems posed. These issues are related, of course, as are all of the four levels. Historically, psychologists have tended to focus on causation and ontogeny (termed *proximate* levels), and biologists have tended to focus on survival value and evolution (termed *ultimate* levels).

The resounding lesson from Tinbergen (1963) is that it is vital to understand at which level you are asking questions, in order to get the right answers. Also important is an acknowledgement that communication operates at all these different levels, and understanding that ultimate aspects might aid understanding of proximate aspects, and vice versa. However, ultimate and proximate explanations are often confused or are used as contradictory alternatives, which they are not (see Chapter 10, for a more detailed discussion).

1.2 What are primates?

The order Primates[1] is a monophyletic group of mammals united by a single common ancestry (Fleagle, 1999; Schultz, 1969). A taxonomic group must be characterized by a set of shared morphological traits possessed by no other group (Mayr, 1963, 1969; Simpson, 1961). These shared specializations, or shared derived features, are called **apomorphic** characters and they help define one taxonomic group relative to others. While behavioural and ecological characteristics are important in helping to create a definition of animal taxa, particularly close attention is paid to morphological characteristics because these will be preserved in the fossil record and will allow the evolution of a taxon to be traced over time. However, one of the problems with primates as an order is that it is relatively difficult to identify a clear fossil record of early primates.

Broadly speaking, primates are defined as an order based upon a general set of morphological and behavioural characteristics summarized in **Box 1.3**. Living primates possess a suite of morphological characteristics that help us unite them into a single order. These characteristics include a grasping big toe (hallux) and thumb (pollex) and low-crowned molars. However, unlike other mammalian orders, primates lack any one shared specialized characteristic that is clear and unambiguous as, for example, the blowhole shared by all cetaceans. The defining morphological features of

[1] Clearly, humans belong to the Primate order and are part of the great ape family Hominidae, along with orangutans, gorillas, chimpanzees, and bonobos (Groves, 2001). However, in this book we use the term 'primates' to refer exclusively to nonhuman primates unless otherwise stated.

Box 1.3 How are primates defined relative to other mammals?

Morphology

- Limbs adapted for prehensile (grasping) lifestyle rather than clinging or clawing
- Grasping pollex (thumb) and hallux (big toe) to enhance prehension
- Nails, not claws, associated with development of tactile pads on hands and feet
- Shortened snout or face
- Binocular vision
- Low-crowned molars, reflecting diet centred more on fruits than grass
- Cerebral cortex expansion with relatively larger head

Behaviour

- Highly social throughout life
- Increased reliance on vision
- Unique reproductive behaviours (see **Box 1.4**)

primates do not come in all at once in the fossil record, leaving us with a mass of fossils that are controversial as to whether or not they are indeed primates.

In addition to the morphological traits summarized in **Box 1.3**, reproductive features including the cyclical nature of female ovulation, pregnancy and the birth process, parental care of offspring and adaptations of offspring for growth and development are also of central importance (**Box 1.4**). An understanding of these life-history patterns in any mammal group is central to an appreciation of the evolution of primate societies and communication (Martin, 1990).

One of the major behavioural traits of primates relative to other mammals is their tendency to be highly social throughout all life stages,[2] an attribute that is reflected in the morphology, behaviour and reproductive features of primates. While many mammals temporarily group together under various circumstances, the associations are typically short term and the individuals involved in the aggregation change over time. In primates, group membership tends to be highly regular (Clutton-Brock and Harvey, 1977; Fleagle, 1999; Sussman, 1999). Because this book is highly influenced by this particular distinguishing characteristic of primates, we focus on how their highly social behaviour influences their life histories and the development and evolution of their communication.

1.2.1 Primate phylogeny

Today, primates naturally occur almost exclusively in the tropical and sub-tropical zones of South America, Africa and Asia. While many aspects of primate taxonomy and phylogeny are hotly debated, living primates are generally grouped into suborders

[2] Exceptions to this include the highly social naked mole rats (Sherman, Jarvis and Alexander, 1991), meerkats (Clutton-Brock *et al*., 2000), hyenas (Kruuk, 1972), wolves (Mech *et al*., 1998), lions (Schaller, 1972) and some cetaceans (Mann, 2000).

Box 1.4 Distinctive features of primate reproductive behaviour

Reproductive organs

Prosimians retain the primitive mammalian condition of a **bicornuate uterus**, while **anthropoids** have developed a **simplex** uterus. This may be related to the reduction in litter size seen in anthropoids, which typically only have one offspring at a time.

Female ovulation

Most mammals are induced ovulators; that is, an ovum is released by the female in response to the act of mating. Primate females are spontaneous ovulators. Females release an ovum at regular intervals regardless of the act of mating. Spontaneous ovulation implies a close coordination between males and females so that the male can detect when the female is in oestrus. This is typically done through olfactory signals (pheromones) but also through visual signals (e.g. sexual swellings in female chimpanzees).

Pregnancy and birth

Female primates have a very long gestation (pregnancy) period relative to maternal weight. This allows the developing foetus to spend a greater period of time developing the large brain that primates are born with, relative to other mammals. Unlike most other mammals, primates typically only gestate a single, high-quality offspring with a high brain weight relative to body weight. Callitrichids, such as marmosets and tamarins, have evolved an interesting reproductive strategy of usually giving birth to twins. This is accompanied by their unusual social system of polyandry, with only one breeding female having access to several males.

Parental care of offspring

Unlike most other mammals, female primates spend a long period of time in postpartum anoestrus while they lactate and suckle the newborn. This investment in a (typically) single offspring at a time requires the mother to stay in close contact with the infant, usually by carrying it whilst the infant clings to the mother's fur until it can begin to feed more independently. This period of intensive investment by the mother often requires provisioning or **allocare** from other social group members in species that live in groups. The callitrichids again have a unique parental care strategy among primates, since they form cooperative polyandrous groups. In these species, the newborns are typically carried by the males or by the nonreproductive females so that the single breeding female can return to oestrus.

Adaptations in the offspring for growth and development

Primate infants are characterized as having a markedly slower postnatal development relative to other mammals, a period where they are learning social behaviours and other skills. This slow period of development has been linked to the relatively late onset of sexual maturity in primates.