Introduction

Welcome to The Cambridge Handbook of Animal Cognition! We hope you will find this a useful reference and a comprehensive overview of a fascinating area of study.

The Handbook is divided into six parts – *Communication and Language*, *Memory and Recall*, *Social Cognition*, *Social Learning and Teaching*, *Numerical and Quantitative Abilities*, and *Innovation and Problem-Solving*. Each of these six parts begins with an overview chapter, which seeks to provide you with a broad background of the history, concepts, and key findings that are important. If you are new to animal cognition, or are a specialist learning about a topic outside your own area of study, this is where to begin. Each overview is followed by four to six smaller entries, in which we have tried to provide a range of interesting and important work for further exploration. If you are intrigued by the overview, these provide more in-depth information. We have tried to provide entries from a variety of species and taxa.

The book opens with a *Communication and Language Overview* by Federico Rossano and Stephan Kaufhold. Beginning with the oft overlooked invertebrate world, Baptiste Piqueret and Patrizia d'Ettorre discuss *Communication in Ant Societies*. Moving on to species that we much more commonly communicate with, Irene M. Pepperberg discusses *Symbolic Communication in the Grey Parrot*, while Katalin Oláh, József Topál, and Anna Gergely bring us information about *Communication in Dogs and Wolves.* The part finishes with a discussion of *Semantic Communication in Primates* from Klaus Zuberbühler.

Gema Martín-Ordás provides the *Memory and Recall Overview*, followed by *A Fish Memory Tale: Memory and Recall in Fish and Sharks* by Catarina Vila Pouca, Louise Tosetto, and Culum Brown. Leaving the water for the air and land, Maria Cristina Tello-Ramos and David J. Pritchard discuss *Memory in Hummingbird*, and Jonathon D. Crystal details *Event Memory in Rats*. Finally, Molly Flessert and Michael J. Beran address *Primate Recall Memory*.

The *Social Cognition Overview* is provided by Juan-Carlos Gómez. Once again, we begin our survey of the area in the water as Joachim G. Frommen and Stefan Fischer present *Proximate and Ultimate Mechanisms of Cooperation in Fishes*. From a slightly different angle, Elena Lorenzi and

1

Giorgio Vallortigara discuss overall *Evolutionary and Neural Bases of the Sense of Animacy*. Thomas Bugnyar addresses *Raven Social Cognition and Behavior*, while Manon K. Schweinfurth discusses *Reciprocity in Norway Rats (Rattus norvegicus)*. The final three entries in this part address capabilities of larger mammals; Elizabeth A. Krisch and Joshua M. Plotnik take us *Exploring the Social Minds of Elephants*, Adam A. Pack presents an entry on *Dolphin Social Cognition*, and finally James R. Anderson and David L. Butler present *Mirror Self-Recognition: Five Decades of Primate Research*.

Rachel L. Kendal gives us an excellent *Social learning and Teaching Overview*, which is followed by fascinating discussion of a behavior that isn't generally the first thing to spring to mind in the area – *Tandem Running Recruitment by Temnothorax Ants as a Model System for Social Learning* by Takao Sasaki and Stephen C. Pratt. Matthew J. Hasenjager and William Hoppitt provide a discussion of *Fish Social Networks*, while Victoria E. Lee, Alison L. Greggor, and Alex Thornton address *Social Learning in Birds*. Finally, Rachel Nelson, Erin Connelly, and Lydia M. Hopper give us an overview of *Social Learning in Chimpanzees*.

The *Numerical and Quantitative Abilities Overview* is provided by Sarah T. Boysen, followed by a discussion of *Numerical Competence in Fish* by Christian Agrillo and Maria Elena Miletto Petrazzini. Rosa Rugani and Orsola Rosa-Salva detail specific spatial issues in their contribution, *Spatial–Numerical Association in Nonhuman Animals*. Finally, Olga F. Lazareva discusses *Perceptual Categorization in Pigeons*.

In the final part, Daniel Sol provides the *Innovation and Problem-Solving Overview*. This is followed by Charles Locurto's discussion of *General Intelligence (g) in Mice*. Moving on to birds, Jason Keagy presents *Bowerbird Innovation and Problem-Solving*, and *Parrot Innovation* is discussed by Theresa Rössler, Berenika Mioduszewska, and Alice M. I. Auersperg. Allison B. Kaufman brings us *Innovation in Marine Mammals*, followed by two sections on primates – *Innovation in Capuchin Monkeys* by Eduardo B. Ottoni and *Innovation and Problem-Solving in Orangutans* by Anne E. Russon. The last two entries in this part provide for a more general approach to the overall idea of innovation and problem-solving. Heidi L. Marsh asks *Do Apes and Monkeys Know what They [Don't] Know? The Question of Metacognition in Primates*, and Francesca De Petrillo and Alexandra G. Rosati present *Decision Making in Animals: Rational Choices and Adaptive Strategies*.

We hope we have provided readers with a strong overview of animal cognition and a broad range of more specific cases and examples. Please enjoy!

PART I

Communication and Language

1 Animal Communication Overview

Federico Rossano and Stephan P. Kaufhold

For one reason or another, you have decided to pick up this book. Assuming that you are reading the printed words and understand English, your motivation to do so is likely to acquire information about the topic displayed on the cover: *animal cognition*. If you want to show this chapter to your pet, they might perceive similar visual stimuli – black symbols on a white page – however, they will not extract the same information as you can. Many human societies have developed writing as a cultural tool that allows transmitting linguistic information beyond the present to a theoretically unlimited number of individuals who are able to read the content. Acquiring the skills necessary for reading and writing is a time-consuming process, and does not come easily to us; mastering this practice takes many years. On an evolutionary scale, representing language through written symbols is a relatively recent invention, and still accounts for only a fraction of the information that we communicate with each other. Notably, our ability to read written symbols relies on cortical areas of the brain that have evolved for object and face visual recognition and clearly not for reading per se (see e.g., Dehaene & Cohen, 2011). Spoken language, in contrast, is not only considerably older, but also a human universal and commonly listed as one of *the* defining abilities of our species. Language enables us to flexibly communicate feelings and ideas with innumerable degrees of freedom. While a communication system as complex as language might be unique to our species, the transfer of information between organisms is a common phenomenon in biology. The study of communication across the phylogenetic tree can not only help to better understand how human language has evolved but is also central to understanding living organisms in general. Depending on the definition, communication is not limited to animal species, but can be found across a wide spectrum of species, such as bacteria and plants. Even communication between different biological kingdoms can be commonly found, and is the subject of a rich body of research literature, for example plant–animal communication (e.g., Schaefer & Ruxton, 2011). This is, however, beyond the scope of this chapter, which will rather provide a brief summary of concepts, approaches, and issues related to the study of communication between animals.

It is important to note that animal communication, like every other biological phenomenon, can be addressed on multiple levels. The most common

framework for explaining behavior on different (but complementary) levels of analyses are *Tinbergen's four questions*. In his seminal paper *On aims and methods of Ethology*, the Dutch ornithologist and ethologist Nikolaas Tinbergen (1963) distinguished between causation, ontogeny, adaptation, and phylogeny. Causation and ontogeny can be grouped as *proximate*, or *how*, questions. Explanations of causation address mechanistic explanations of behaviors, that is, they address the question: "*How does it work?*" For example, how do certain muscle movements bring about observable behavior? Ontogeny refers to the development over the lifespan of an individual and thus addresses how a behavior develops and changes over the life course of an animal. Proximate questions can theoretically be observed by studying one individual longitudinally. In contrast, adaptation and phylogeny are categorized as *ultimate*. or *why*, questions, that is, questions that relate to the evolutionary origins of behaviors. These questions, therefore, address evolutionary timescales across many generations. The question of *adaptation* asks if and how certain behaviors have contributed to the reproductive success (i.e., the likelihood of producing viable offspring) of an individual's ancestors. Colloquially, adaptation inquiries could be translated into the question: "*What is it good for*?" Given that evolution through natural selection operates through making gradual changes to preexisting structures, the question of *phylogeny* addresses precursors and origins of the phenomena under question in the ancestral lineage of an organism by asking the question, "*Where did it come from*?"

We broadly divide this chapter into two sections. First, we focus on ultimate explanations for animal communication. Then, we continue with some proximate explanations for animal communication. Historically, the study of animal communication started with a focus on the phylogeny of animal communication, but in recent years proximate mechanisms have received increasing attention.

Why Do Animals Communicate? (Ultimate Explanations)

We start by briefly outlining some ultimate explanations (evolutionary causes) as to why animals communicate with each other in the first place. In general, natural selection can produce organisms with perceptive and cognitive skills that enable them to acquire information about their environment. Obtaining information about the environment through phylogenetic and ontogenetic processes allows organisms to behave in ways that increase their chances for survival and reproduction. Through adaptations to the environment, natural selection thus produces organisms that indirectly represent properties of the external world that affected the reproductive success of their ancestors. Lorenz, for example (1941, 1973), illustrated this process through his example of the evolution of the fins of a fish. Over the course of

phylogeny, fins were shaped by the physical properties of water, and thus contain information about water that was relevant for the survival of the ancestral lineage of fish. The properties of water are a stable aspect in the environment of many aquatic animals, therefore structures analogous to fins that enable moving efficiently in water can be found across many species, such as cetaceans and penguins. The degree to which aspects of an organism's environment remain stable throughout phylogeny and ontogeny are related to the nature of adaptations. Environmental properties that remain stable across phylogeny can be matched by adaptations that require little flexibility, whereas less stable properties of the environment might require more flexible adaptations in the form of physiology, perception, cognition, and behavior. The behavior of other organisms – both conspecifics and different species – is an influential environmental factor for most animals, which exerts great influence over their reproductive success. Because the behavior of organisms can influence each other, many of their relationships can be bidirectional and will therefore create positive feedback loops on their evolution. Note that the relationship between certain physical aspects of an environment and an organism might only be unidirectional. Take the example of aquatic animals and water – while the properties of water affected their evolution, the same is not true for the opposite direction. However, organisms can adapt to each other's behavior through both phylogenetic and ontogenetic mechanisms. The relationship is therefore often bidirectional and can lead to evolutionary arms races (Dawkins & Krebs, 1979). Dynamics like these have been extensively documented and researched in animal communication.

One of the first systematic studies of animal communication was developed within the field of ethology, which mainly focused on the phylogeny, the ancestral origins of communicative behaviors. For example, Konrad Lorenz was interested in reconstructing the phylogeny of behaviors by focusing on display patterns (e.g., threats and courtship displays) across different species. While behaviors themselves do not fossilize, comparing behavior patterns of extant species is one way of tracking phylogenetic relationships through homologies. This behavioral approach allows reconstructing shared ancestral behaviors across animal species. One of the reasons Lorenz focused on communicative, ritualized behaviors was their conspicuous nature. According to Lorenz (1966), one of the most important characteristics of a phylogenetically ritualized behavior is that a motor pattern that originally served a noncommunicative function in the environment changed in a way that it also served a new communicative function. This is similar to Tinbergen's (1952) work on *derived activities,* which drew on insights from his extensive work with birds. Much of Lorenz's research on animal communication focused on backtracing the behaviors and motivational conflicts that eventually led to the development of communicative signals. According to him, many signals initially evolved from intention movements, that is, movements that precede a

behavior, or displacement activities, behaviors that are performed as a result of opposing motivational drives (e.g., fighting vs. fleeing).

More broadly, most organisms have to acquire information about their physical and animate environment throughout their lifetime in order to survive and reproduce. Danchin and colleagues (2004) divide the information that individuals acquire about their environment into *personal information* and *social information*. Personal information refers to information that an animal individually acquires about its environment, for example through direct perception of, and interaction with, the physical world, like trial-and-error-learning. In contrast, social information refers to all information acquired through observing other organisms. Social information can be about the physical environment, or about properties and states of other organisms. Social information can be further categorized into *cues* and *signals*. Cues are also referred to as inadvertent social information because they are not shaped by natural selection to be picked up by other organisms. Nonetheless, they might be picked up by others, which might result in negative, neutral, or positive outcomes for the cue producer. For example, imagine yourself walking down a muddy trail. On your way, you encounter bear tracks in the mud. This is a cue that might lead you to change your walking direction in order to prevent an unwelcomed encounter with a bear. However, the bear's tracks are just a by-product created by its movement through the muddy terrain, and are not left by the bear in order to be perceived by you. Generally, both the ultimate and proximate reasons for the occurrence of cues do not involve providing information to others. Instead, the information that might get picked up is simply a by-product of other activities. In contrast, animal signals are acts or structures that evolved for the "specific purpose of conveying information and thereby influencing others' behavior, ultimately impacting both the signaler's and the recipient's fitness" (Laidre & Johnstone, 2013, R831). Therefore, animal communication occurs when a sender transmits a signal with the goal of influencing the behavior of at least one receiver. Many signals originated from acts or structures that once were cues. It is possible for cues to evolve into signals if they – on average – provide benefit for both the sender and the receiver (Laidre & Johnstone, 2013). Signal design is always the outcome of a bidirectional relationship, meaning it is influenced by the selective pressure applied to both the signaler and the receiver (Johnstone, 1997).

Signals can further be distinguished based on the kind of information that is communicated. Maynard Smith and Harper (1995) distinguish between *self-reporting signals*, which "provide information, positive or negative, about some property of the signaller" and *other-reporting signals*, which provide "information about an object or organism other than the signaller" (p. 307). Warning coloration, also referred to as aposematism, is one example of a self-reporting signal that can be found in many prey species that protect themselves against predators by producing poison. Not only does the poisonous prey benefit from not getting eaten, but the predator also benefits from not

getting poisoned. Therefore, selective pressure is put on both individuals to establish a signal that prevents this from happening. The prey species therefore benefits from exploiting the predator's vision and psychology in order to generate a conspicuous warning coloration that can easily be recognized (Stevens & Ruxton, 2011). For example, many poison frogs (*Dendrobatidae*) have conspicuous coloration and patterns on their bodies that are meant to be detected by potential predators (Santos, Coloma, & Cannatella, 2003; Darst, Cummings, & Cannatella, 2006). In contrast, alarm calls are an example of an other-reporting signal that can be found in many mammal and bird species. Some of these gregarious animal species will produce calls that inform conspecifics about the presence of predators. One well-studied example is the alarm calls produced by vervet monkeys (*Cercopithecus aethiops*). Notably, these primates do not only produce one type of alarm call, but instead will produce different alarm calls associated with the detection of different predators, such as leopards, snakes, and hawks. Each call will elicit a different fleeing response in the monkeys that is appropriate for avoiding attacks by specific predators (Seyfarth, Cheney, & Marler, 1980). For example, the monkeys respond to the leopard alarm call of conspecifics by seeking shelter in trees.

The examples of alarm calls and warning coloration illustrate that signals can develop within cooperative relationships, such as informing conspecifics with alarm calls, but also within competitive contexts, such as warning colorations that are meant to deter predators. In order to be effective, signals should be designed in a way that they can be easily detected, discriminated, and remembered by receivers (Guilford & Dawkins, 1991). In other words, efficient signals can decrease the perceptual threshold and cognitive effort that is needed by the receiver to pick up information. Therefore, communication can package information in a more accessible way through both reducing the perceptual threshold and the cognitive effort of receivers to gain access to information about their environment. Notably, this highlights that signals are not optimized to transmit information in absolute terms, but rather in the most accessible way based on the perceptual and cognitive systems of the receiver. This can explain why many signals contain redundancy and make use of different modalities simultaneously.

There is a great diversity of perceptual abilities across the animal kingdom, corresponding to a broad range of modalities that are used for transmission. Bradbury and Vehrencamp (1998) provide a detailed overview and discussion on the mechanics and different modalities associated with signal transmission in animals, for example through auditory, visual, and chemical channels. Signals vary widely in their duration, oftentimes associated with the medium through which they are transferred. While acoustic signals, such as alarm calls, might be highly transient and fleeting, other signals, such as the warning colorations against predators, can be inflexible and enduring throughout most of the life of the signaler. Moreover, signals tend to be produced with a *typical*

intensity and a typical frequency or duration, so as to facilitate recognition and reduce signal ambiguity (Morris, 1957). Flexibility and variability occur in special situations that require the production of signals louder, longer or more often, for example to convey urgency or danger. Imagine somebody calling your name to summon you to do something, and under which conditions they would be calling you more loudly (e.g., because of urgency or because you seem distracted) or more softly than usual (e.g., to make the summoning less public, possibly to hide it from possible overhearers).

The signals used for alarm calls and warning coloration do not only differ with regard to their durations, but also with regard to the relationship with the receiver. While some are directed towards conspecifics, for example courtship displays, others can be directed towards members of different species, such as in the example of warning coloration against potential predators. According to signaling theory, signals can emerge as long as they provide, on average, benefits to both the signaler and the receiver, regardless of the nature of the relationship. One striking example for interspecific communication is the symbiotic relationship between humans and greater honeyguides (*Indicator indicator*). These birds can be found in sub-Saharan Africa and acquired their name from their ability to lead humans (such as the Boran people of Kenya) to bees' nests. Honeyguides produce acoustic and visual signals to inform humans about the location of bees' nests that they have spotted. Both parties mutually benefit from this relationship (Isack & Reyer, 1989). Honey gatherers reduce their time searching for bees' nest when they are being guided by the honeyguide. In return, the birds gain easier access to the beeswax and larvae and have a reduced risk of getting stung by bees, because the humans use fire during the extraction of honey. Both humans and honeyguides produce specific calls during the honey search that are recognized by the other species (Spottiswoode, Begg, & Begg, 2016). This symbiotic signal exchange is possible because the auditory perceptual spectra of humans and honeyguides overlap sufficiently to recognize each other's calls.

However, not every relationship between senders and receivers with overlapping perceptual spectra ends up being symbiotic. Animals can also "listen into" calls produced by third parties in order to gain social information. Eavesdropping occurs when organisms use cues or signals from other organisms to their benefit for which they are not the intended receivers (Bradbury & Vehrencamp, 1998) and thus is a form of social information. Therefore, the extent to which producing a signal is beneficial to the signaler is not only based on the responses of intended receivers, but also potentially by the responses and behaviors of eavesdroppers. As such, selective pressure on the design of signals is not only a result of the interaction between senders and receivers, but also based on the responses by eavesdroppers. If senders produce signals that would commonly be used by eavesdropping predators to locate them, the risks of producing the signal might exceed the potential benefits for the sender. However, eavesdropping does not necessarily result in negative consequences

for senders or receivers. For example, Potvin and colleagues (2018) showed that wild-superb fairy-wens (*Malurus cyaneus*) can learn to associate alarm calls from other species with predators through acoustic learning when they co-occur with alarm calls with which they were already familiar. Wild superb fairy-wrens therefore eavesdrop on other species' alarm calls, which is not necessarily disadvantageous for the heterospecific callers. Eavesdroppers can be both individuals from the same species as the sender of the signal and individuals from different species, such as the example with the fairy-wrens described. In the case of eavesdropping, an animal intercepts the communication between third-party senders and receivers. In principle, the fitness consequences can be on average positive, negative, or neutral for the intercepted parties.

Additionally, animal communication systems are also vulnerable to deception, both within and between species. Animals may find themselves in a broad range of situations in which the production of and response to a signal is beneficial to them but not necessarily the receiver. According to Searcy and Nowicki (2005) (who use a slightly modified definition by Mitchell (1986)) deception occurs when a "receiver registers something Y from a signaler; the receiver responds in a way that benefits the signaler and is appropriate if Y means X; and it is not true that X is the case" (p. 5). For example, female fireflies of several *Photuris* species mimic the sexual flash signals of females from other firefly species, for example, *Robopus* and *Photinus*, in order to lure in males from those species and prey on them (Lloyd, 1983; El-Hani, Queiroz, & Stjernfelt, 2010). The males register what they interpret as a sexual signal by female conspecifics, and therefore approach the flash signal, which would be an appropriate (i.e., adaptive) response if it were indeed produced by a female of their own species and not a deception by another species of fireflies. Another example of deception can be found in brood parasites, with the most famous example being the cuckoo (*Cuculus canorus*), but also some species of the previously mentioned honeyguide. Brood parasitism substantially reduces costs of parental investment: The females of the parasite species lay their eggs in the nests of other species. If the brood parasite succeeds, the host species will feed and raise the hatched chick as their own. The fact that animal communication systems can be susceptible to deception raises the question of how reliable signals can persist nonetheless, particularly in situations where a sender could derive benefits from deceiving. Zahavi (1975) provided one possible answer, by introducing his concept of *honest signals* along with the notion of the *handicap principle*. According to this view, signals that are costly to the signaler, and thus cannot effortlessly be produced (they constitute a handicap for the signaler), can be considered "honest." Through increased costs, the signals become less likely to be deceptive because the reproduction costs would be higher than the gains of faking it.

Signals can be costly in different ways, such as the amount of effort needed to produce them, the increased likelihood of detection by individuals other