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The Routledge International Handbook of Comparative Psychology

Edited by Todd M. Freeberg, Amanda R. Ridley and
Patrizia d'Ettorre

THE ROUTLEDGE INTERNATIONAL HANDBOOK OF COMPARATIVE PSYCHOLOGY

The Routledge International Handbook of Comparative Psychology is an international reference work that offers scientists and students a balanced overview of current research in the field of comparative psychology and animal behaviour.

The book takes an integrative approach to animal behaviour, with most of the chapters discussing research involving both proximate (developmental and mechanistic) and ultimate (functional and phylogenetic) levels of analysis. Chapters cover the major ideas of core topics in the field and examine emerging research trends to provide readers deeper understanding of these ideas. One of the strengths of this book is its coverage of core topics in comparative psychology and animal behaviour from different – and diverse – perspectives. The diverse perspectives come from the wide range of focal species studied by chapter authors, a range traditionally quite atypical for comparative psychology, and from the widespread international representation of the authors and the diversity of departments and research centers at which these authors work. The first part of the *Handbook* examines historical and foundational principles and theories in the field. The second part focuses on individual behaviour systems. The final part of the book is devoted to a diversity of ideas that extend our understanding of behaviour into new directions.

The Routledge International Handbook of Comparative Psychology is an essential resource for advanced undergraduate and graduate students, postdoctoral researchers, and established academics, as well as others who are interested in comparative psychology and animal behaviour.

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We dedicate this book to the memory of the remarkable Dr Julie Morand-Ferron, whose exceptional cognition research is presented in this book.

Todd would like to dedicate this book to Daniela Corbetta and Maya Corbetta-Freeberg, who make every day better.

Patrizia would like to dedicate this book to her mother, Antonetta, who passed away in January 2021.

Mandy would like to dedicate this book to her ever supportive and loving family, particularly her sons Caelan and Kito who tolerated her many hours on the computer. Mandy would also like to dedicate this book to the many research assistants, postgraduate and postdoctoral students that dedicate so many hours in the field to furthering our knowledge and advancing our scientific understanding.

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PART 1

Foundations

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INTRODUCTION TO THE *ROUTLEDGE INTERNATIONAL HANDBOOK OF COMPARATIVE PSYCHOLOGY*

Todd M. Freeberg, Amanda R. Ridley and Patrizia d'Ettorre

Comparative psychology has a long history in the study of animal behaviour. The term 'comparative psychology' has meant many different things to different researchers in the field over this long history (see Chapter 1; Dewsbury 1984; Greenberg & Haraway 1998; Burkhardt 2006; Call et al. 2017). The traditional view of comparative psychology from the middle of the 1900s contrasted it with ethology as an academic discipline (Burkhardt 2006; Burghardt & Bowers 2017). According to this traditional view, while ethologists generally focused on species-typical and fitness-related behaviour patterns of a wide range of species in their natural habitats, comparative psychologists generally focused on broad mechanisms of learning and the physiological underpinnings of behaviour in a few focal species in highly-controlled experimental laboratory settings. Today, even a glance at the top journals in the field of animal behaviour indicates that this traditional view is largely a thing of the past. Journals that historically had more of a behavioural biology orientation, such as *Ethology* and *Behavioural Ecology*, now regularly publish articles in which learning and cognition are a primary research focus. Journals that historically had more of a psychology orientation, such as the *Journal of Comparative Psychology*, now regularly publish articles on fitness-related behaviour of a wide array of species in natural (non-laboratory) settings. Indeed, a recent review of this "flagship" journal in the field of comparative psychology indicates the wide breadth of research subjects and foci of study in the field today – whereas rats were the focal species of study in roughly 60% of the papers published in the journal from the 1930s to the 1970s, today non-human primates, non-primate mammals, and birds together reflect the focal species of study in roughly 70% of the papers published in the journal (Snowdon 2021).

How the *Routledge International Handbook of Comparative Psychology* contributes to the changing research focus

We view comparative psychology today as no more and no less than the study of animal behaviour with, perhaps, slightly more emphasis on learning and cognition than other sub-disciplines within the broad field of animal behaviour (Dewsbury 1984). Over a century ago, some foundational researchers viewed comparative psychology as the study of behaviour of non-human animals (Yerkes 1908), whereas others viewed it as the study of behaviour of all animals, including our own species (Morgan 1894). Early on, the emphasis was placed strongly upon *comparative research* for many in the field – we would gain deeper understanding of the major drivers of behavioural variation by assessing similarities and differences across multiple species (e.g., Schneirla 1952). This view did not become the core organizing principle in comparative psychology, however, as the field shifted its focus in

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the early- and mid-1900s largely toward just a few species – rats, pigeons, and humans (Burghardt & Drickamer, this volume; Lorenz 1950).

A foundational perspective to the study of animal behaviour, shared by current research in comparative psychology, is the framework built by Niko Tinbergen (1963). Research questions in animal behaviour can take proximate approaches focused at the individual level. One of these involves immediate causation, the current (internal or external) stimuli and mechanisms driving behavioural change. The other proximate approach involves ontogeny, the past experiences and developmental processes that caused behavioural change. Research questions in animal behaviour can also take ultimate approaches focused on the population. One of these involves adaptiveness, the current selection pressures operating on populations to drive behavioural change. The other ultimate approach involves phylogeny, the past histories of common ancestry that caused behavioural change in an evolutionary lineage. As Tinbergen's own body of research revealed, integration of two or more of these four levels of analysis in a research program can lead to deeper insights and understanding about what causes behavioural variation within and across individuals and populations. This integration was in fact a central organizing principle behind an important edited volume in comparative psychology that was published over three decades ago (Dewsbury 1990). **One of our aims with this *Handbook* was therefore to include contributors and research programs that collectively, if not individually, integrate these different levels of analysis described in the Tinbergen framework**.

Like many fields in the sciences, animal behaviour research was carried out for decades largely by white men from Europe and North America (Boakes 1984; Dewsbury 1984). Recent reviews of the field indicate that this is changing (Lee 2020, Snowdon 2021). Like many fields, comparative psychology and animal behaviour are growing stronger and more vibrant as they grow more diverse and inclusive. We believe an important strength of our *Handbook* is the coverage of standard topics in comparative psychology and animal behaviour, but from very different perspectives. The diverse perspectives in our *Handbook* come from the extremely wide range of focal species studied by the chapter authors, a range that, traditionally has been quite atypical for comparative psychology. Our inclusion of bright early career researchers and internationally recognized senior scientists amongst our contributors will help to engender a very contemporary feel to a substantial part of the research that is described in the *Handbook*. We believe that this will be welcomed by readers around the world at all levels, from students to senior faculty. Most of the continents are represented in the chapter contributions, reflecting the full breadth of research that is currently taking place in comparative psychology and animal behaviour. Furthermore, the co-editors in and of themselves come from three different continents. **Another aim for this *Handbook* was to create a volume that would be of wide international interest and use, both for its coverage of major topics in the field of behaviour, as well as the diversity of authors involved**.

This *Handbook* is structured into three main parts. In the first part, authors lay out some of the foundational views of behaviour and ways of studying behaviour, including historical perspectives in terms of theory and method, as well as key topics that emerged over the past decades. The last part includes important ideas that have extended and complicated (in ways healthy to our science!) our views of proximate and ultimate approaches to understanding behaviour. The middle part examines different behaviour systems. Since this might seem an atypical way to compose this middle part of the book, we thought it worth describing the "behaviour systems" view here briefly.

Behaviour Systems

A theoretically powerful way of conceptualizing and empirically studying behaviour that emerged in the middle part of the 1900s involves what is now called a behavioural systems view. The behavioural systems view understands different behavioural acts of organisms as being units in larger functional systems (Burghardt & Bowers 2017). Oftentimes these units are produced in species-typical sequences with other units to meet the particular needs of the individual (Timberlake & Lucas 1989). These behaviour systems relate ultimately to the survival and reproductive success of the individual. In an early example of this kind of view, Tinbergen (1942, 1951) described the reproductive needs of stickleback fish as being influenced by at least four different behaviour systems (Figure 0.1). Each behaviour system comprises a number of fairly discrete behavioural units (Tinbergen labelled these each as a "level of the consummatory act"). Important extensions of this basic model were made by Timberlake and colleagues to include appetitive processes (e.g., general and focal search), to stress the fact that higher unit structures can map on to more than one lower unit and lower units can relate to more than one higher unit structure, and to make clear the flexibility of the structures and their openness to learning (Timberlake & Lucas 1989; Cabrera et al. 2019).

Different motivational, emotional, and physiological states often underly different behaviour systems (Burghardt 2019; see Chapter 6). An important implication of the behaviour systems view relates to the notion of conflicting motivations (Craig 1918). For example, during key stages of breeding seasons in many species, behaviour systems like aggression and courtship can take precedence over behaviour systems like sleep, eating and drinking, and avoiding predation.

Early notions of behaviour systems largely viewed systems as being composed of mutually exclusive behaviours (Tinbergen 1951; Baerends 1976). Hogan (1988) advanced our understanding of behaviour systems by developing theoretical models of how stimuli activate perceptual mechanisms of organisms, which activate higher level central mechanisms, and both these perceptual and central processes influence the motor patterns underlying the behaviour that is generated. (Note that in this view of behaviour systems, "mechanism" does not necessarily imply a neural mechanism – Hogan 2015.) Importantly, the same behaviour units can be activated by different stimuli and by different perceptual and central mechanisms such that a single behaviour unit can be involved in different behaviour systems – for example, stalking behaviour in both felid predation and play behaviour systems.

Although behaviour systems thinking largely emerged from ethological foundations, experiential factors in development became crucial to its advance (Hogan 1994). Though there were many different approaches to learning taken in comparative psychology and related fields, the one with deep relevance to behaviour systems is advocated by Tinbergen (1951) – to understand what animals actually *do* learn in their natural environments rather than what they *can* learn in perhaps highly artificial and arbitrary laboratory environments. Indeed, the integration with learning was central to Timberlake's (1983) view of behaviour systems – "an organism is viewed as a set of organized and interrelated

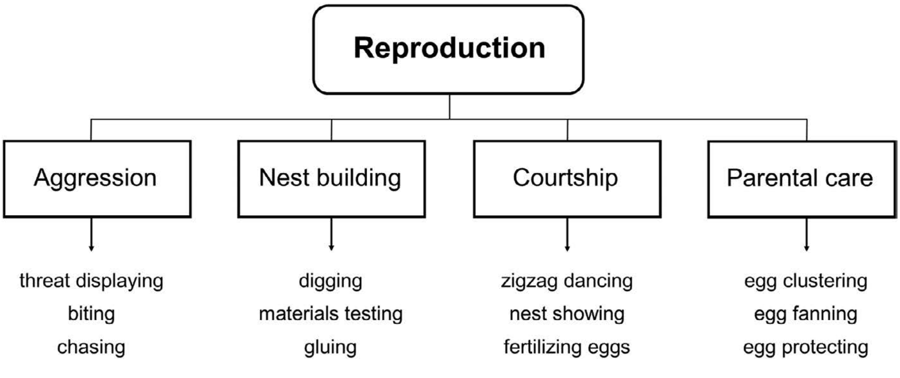

Figure 0.1 Example of a set of behaviour systems related to reproduction in stickleback fish, with a few examples of behavioural units involved in those systems.

Figure redrawn from Tinbergen 1951.

regulatory systems that precede, support, and constrain learning" (Timberlake & Lucas 1989, p. 237). Taking a behaviour systems view of learning requires that experimental apparatus and stimuli be centered in the particular ecological problem space faced by the species under study (Burghardt & Bowers 2017). Moreover, behaviour systems approaches to certain 'anomalous' learning outcomes can help to reveal how those outcomes tend to fit with the ecology or evolution of the species under study, as well as with our understanding of learning processes (Killeen 2019; Zentall et al. 2019).

Overview of Chapters

Our journey starts by taking an historical perspective on comparative psychology, ethology and behavioural ecology but with an open eye on the future of these disciplines, and a discussion about how to develop viable integrative approaches (**Chapter 1)**. A summary of the history of behaviourism and its critical development is the focus of **Chapter 2**, with examples of how basic work in the behaviourist tradition has promoted our understanding of the neural basis of acquired behaviour, new developments in pre-clinical research and comparative cognition. Ethology developed from direct observation of animals in the field, while comparative psychology became focused on the study of animals in a lab. Between these two extremes there are several other alternatives that incorporate the best of both worlds. These methodologies are examined and discussed in **Chapter 3**. The behaviour of an organism can be shaped by stimuli experienced even before birth and the ontogeny of behaviour is a phenomenon that continues throughout the entire lifespan. **Chapter 4** gives an overview on the development of behaviour with examples from insects to birds and mammals.

We can appreciate the different ways animals experience the world only by understanding their sensory and perceptual experiences. **Chapter 5** presents the diversity of sensory and perceptual systems both within and among phylogenetically diverse species and the adaptive value of these systems. What are the factors that motivate an organism to initiate and terminate a behaviour? Motivation is the focus of the first part of **Chapter 6**. Motivated behaviours are often associated with emotions. The second part of this chapter discusses the concept of emotion in humans and non-human animals. Understanding the evolution of cognition is possible only with a comparative approach. **Chapter 7** presents an historical background of the field of comparative cognition and discusses its insights and challenges. Integrating proximate and ultimate explanations to understand individual variation in cognition is the focus of cognitive ecology. **Chapter 8** reviews the history of this emerging field and proposes future work aiming at uncovering links between the environment, cognition, and evolution.

The second section of this *Handbook* focuses on specific behaviour systems, and opens with a contribution on how and why animals select specific portions of their environments. Based on field studies, the chapter exemplifies how to investigate habitat selection and its role in conservation biology and restoration ecology (**Chapter 9**). How can we achieve a comprehensive understanding of foraging behaviour? **Chapter 10** reviews important conceptual developments to study foraging across a wide range of species and then focuses on studies on bees as examples of modern integrated approaches to investigate foraging. Avoiding predators and competitors is essential for survival. **Chapter 11** reveals the proximate determinants of vigilance behaviour, from hormones to specialized brain cells and cognitive processes.

Chapters in the second section next shift to focus on behaviour systems that are inherently social. Signals are the basis of communication and they can be extremely complex. **Chapter 12** explores the diversity of animal signals, their transmission, and the role of sensory systems and cognitive processes in shaping the evolution of signals. The next contribution is on intraspecific aggression and its relation to reproductive success (**Chapter 13**) with an overview of neuroendocrine mediators. It then presents the case of exceptional mammalian species, in which females are aggressively dominant over males, as 'experiments of nature' to study the role of androgens in female aggression. **Chapter 14** starts with an historical perspective on the study of mating behaviour and then digs into modern theories that challenge established ideas by suggesting, for instance, that stochastic demography affects mating irrespective of sex. In several species, parental behaviour is essential for offspring survival. **Chapter 15** reviews how parental behaviour is regulated at the hormonal, neural, and sensory level and the mechanisms involved in parent-offspring recognition. An intriguing behaviour is play. **Chapter 16** reconsiders the definition of play and then focuses on playfighting and its role in the development of the social brain and complex forms of communication.

The third part of this *Handbook* is devoted to a diversity of ideas that extend our understanding of behaviour into new directions. We start by asking what cooperation is, and why it happens. **Chapter 17** considers the theories developed to explain cooperative behaviour, and discusses the evidence for direct versus indirect benefits of cooperation, the relationship between cooperation and cognition, and cooperation and environmental conditions. Cetaceans offer striking examples of animal culture, which are summarized in **Chapter 18**. Long-term field observations combined with modelling and laboratory studies reveal multiple aspects of these animal cultures in impressive detail, and provide insights into cultural evolution and gene-culture coevolution in our own species. **Chapter 19** is dedicated to tool use by non-human animals in the wild and in experimental settings and then focuses on how tool use in rats can help us understand the neural mechanisms of tool use in animals and to develop animal models of tool use disorder observed in human patients with ideational apraxia. Language is traditionally considered unique to humans, but **Chapter 20** explores the limits of this uniqueness by giving examples from recent findings bridging the gap between human language and animal communication. What are the evolutionary origins of human decision making? **Chapter 21** explores reasoning and decision making under risk in apes and how they can use a process resembling conditional probabilities typical of humans. There are cases in which an animal manipulates the behaviour of another to the manipulator's benefit, by using dishonest communication. The focus of **Chapter 22** is on deception, how it evolves and persists within communication systems, and the cognitive mechanisms responsible for this intriguing behaviour.

Consistent inter-individual variation in the expression of behaviour is widespread in non-human animals, but what are the ecological causes and evolutionary consequences? **Chapter 23** discusses the adaptive explanations of animal personality with examples from wild rodents and birds. The behaviour of individuals is affected by the presence of other individuals. **Chapter 24** takes a proximate approach to the question of social contextual influences on behaviour, with examples from studies on how variation in flocks influences individual behaviour in chickadees. Some species have more complex social structures than others, but why? **Chapter 25** explores social organization and highlights advances in two animal social systems, using examples of both cooperation and conflict networks. Male-female interactions occur in different demographic, social and environmental contexts, which may influence mating systems. **Chapter 26** explores ecological, social, behavioural and neurogenetic influences on mating systems and then reveals the complexity of mating systems with the example of prairie voles (*Microtus ochrogaster*). Are there features specific to humans in mate choice? **Chapter 27** summarizes current knowledge on human mate choice and commonalities with other species, reviews the concept of mate preferences and how these develop, and presents the most prominent mate choice models. Once a couple is formed, it can either stay close to the family or disperse. The focus of **Chapter 28** is to discuss the comparison of cognition in humans and other species and the insights that can be generated through these kinds of comparisons.

In this *Handbook*, we sought to balance a wide range of topics concisely in chapters that briefly cover major topics in the field but that also allow authors to dive into some of their own work with some depth. **A final aim of ours for this *Handbook* therefore was to have relatively short but detail-rich chapters and a relatively concise overall length. Our hope is that this approach will help make the *Routledge International Handbook of Comparative Psychology* an**

ideal resource for instructors and students (undergraduate and graduate) in class settings ranging from large lecture halls to small discussion sections.

The Editors

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HISTORICAL PERSPECTIVES ON COMPARATIVE PSYCHOLOGY AND RELATED FIELDS

Gordon M. Burghardt and Lee C. Drickamer

Observations of animals in their natural environments have roots in antiquity and were part of daily life and successful hunting, fishing, avoidance of predators, and animal domestication. Recorded observations of animal behaviour go back almost to the beginning of writing; observations of varying accuracy are recorded in Aristotle, Pliny, and even earlier writings from Egypt, Israel, China, and other ancient civilizations. However, systematic observation and formal experimentation began to flower in the sixteenth century with the advent of printing and ready dissemination of findings, although Frederick II's *The Art of Falconry* (1943) from the 1240s is laudably accurate and objective in an era of superstition, anecdote, and anthropomorphism that remained largely unchallenged until the post-Darwinian period. However, superstitions involving animals are still widespread and in scientific research, anecdotal evidence and anthropomorphism are still with us to varying degrees today. Formally, comparative psychology, as an identified field, originated with the writings of George John Romanes (1848–1894) and Conwy Lloyd Morgan (1852–1936) in the late nineteenth century. Earlier authors certainly did important basic work and much of this is recorded in Hess (1962) and Sparks (1982), although there were many additional early contributors in France, Germany, Italy, England, and other countries including travelers, explorers, and collectors. While much of this work was descriptive natural history, experimental research was already taking place as in the seventeenth-century work of Francisco Redi and mid-eighteenth-century studies of Lazzaro Spallanzani, who basically discovered echolocation in bats.

The more recognizable scientific study of animal behaviour began by the late eighteenth and early nineteenth centuries (Drickamer 2010) and became prominent by the mid-nineteenth century, encompassing several approaches. Current studies of animal behaviour can be viewed as a pattern of viewpoints and methods woven into a tapestry. The main threads are ethology, comparative psychology, and behavioural ecology with neuroscience, anthropology, and philosophy playing important roles at various junctures. They intersect at many points and each has sub-threads that hold the main themes together. In combination, they provide an appreciation of both the underlying physiology and development of behaviour, and the patterns of ecology and evolution that define the functional aspects of behaviour. Comparative psychology, behavioural ecology, and ethology all had their origins in natural history and in observations of captive animals including pets and livestock, but diverged and reconnected in varying and often changing ways, a story far too complex to detail here, although some important resources are cited. We will first give capsule summaries of ethology and behavioural ecology before focusing on comparative psychology, and its prominent subfield, comparative cognition. The articles in the recent (2019) *Encyclopedia of Animal Behaviour* cover some of the history in depth on these topics, so ethology and behavioural ecology will be treated briefly. We will focus more

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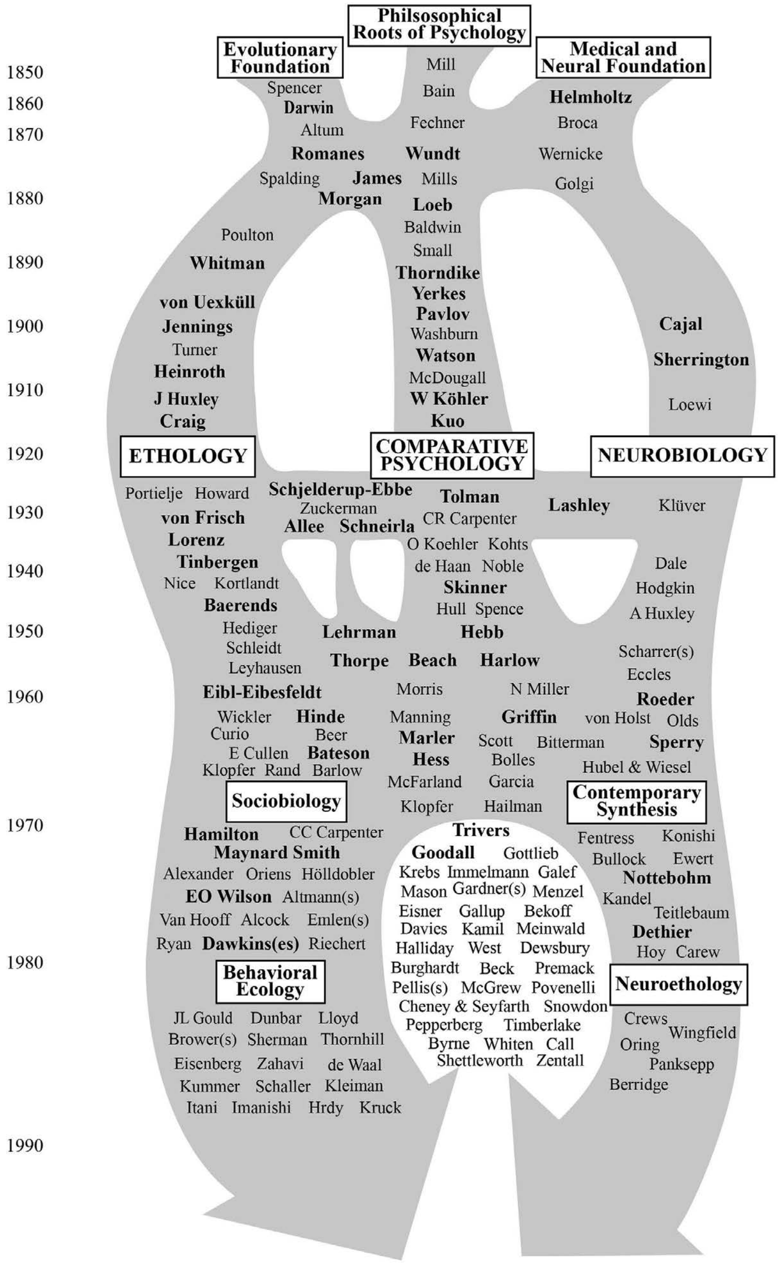

Figure 1.1 The descent of behavioural biology. A subjective impression of the history and relationships of the major disciplines contributing to animal behaviour depicted as an abstract of a historical structure better represented by three or more dimensions. Based on a diagram published in Grier and Burk (1992: 32), it still ends in the 1980s and represents the trends as viewed at that time. However, the diagram has been edited to show how the fields, viewed today, are now converging. Many contributors representing various aspects of animal behaviour and comparative psychology have been added, especially to those who made contributions in the 70s and 80s. Note that with the growth of the fields, many important individuals could not be included and also that many careers were decades long and thus their placement is somewhat arbitrary.

on the topics, concepts, and research approaches and their shifts rather than on the contributions of specific individuals. The latter have been done in depth in the books we cite. A figure summarizing major contributors in the strains leading to modern animal behaviour up to the 1980s is depicted in a diagram modified from a 1992 textbook (Grier & Burk 1992) (Figure 1.1).

Comparative Ethology

The early history of ethology has been recounted from various perspectives repeatedly including by the senior author and will not be detailed here except in brief. (e.g., Thorpe 1979; Burkhardt 2005).

Ethology derived from Darwin's chapter on instinct in *On the Origin of Species* (1859) where he used the comparative method to postulate how such behaviours as slave-making in ants and hive construction in honeybees could have evolved. He also used the comparative approach in showing how domestication for different human uses led to divergent behaviours in different breeds of dogs (pointing, herding) and pigeons (pouting, tumbling) and how these were exaggerations of instinctive behaviours already present in the ancestral stocks. Although not ruling out Lamarckian inheritance of acquired characteristics, he viewed natural and artificial selection as the major factors in formation of species and breed differences. C. O. Whitman in the US and his students similarly focused on species-typical behaviour seen in captive animals and utilized careful observation and description of behaviour along with the comparative method. Poulton (1887) combined experimental methods with predators, such as lizards, in documenting the role of mimicry and animal coloration. Previously, in the 1870s, Spalding experimentally explored the importance, or not, of experience in the development of species-typical behaviour in birds, pigs, and other animals. They were less interested in both animal learning or applied 'principles' developed from non-human animal studies to humans. Somewhat independently, individuals such as Oscar Heinroth, Jakob von Uexküll, Julian Huxley, and others applied the comparative method to understand the sensory and perceptual worlds of animals, the origins of displays, and the sequential organization of behaviour. Many seminal early contributions by these authors were collected and translated in Burghardt (1985).

This approach reached major fruition in the studies of Konrad Lorenz and Niko Tinbergen and their students and colleagues in developing what can be termed classical ethology (Burkhardt 2005). Due to their work, instinctive and innate behaviour became revitalized topics in animal behaviour. They pioneered work on specialized perceptual signals called sign stimuli, coordinated complex movements, labeled fixed action patterns, the hierarchical organization of behaviour, and specialized learning processes such as filial and sexual imprinting, search images, and orientation landmarks. They also developed experimental methods to assess behaviour and its development. The deprivation experiment, where animals were reared without access to certain stimuli during ontogeny, was used to counter arguments that conditioning and other types of learning were involved in much species-typical behaviour. Under criticism from psychologists such as Lehrman, Beach, Hebb, and others, ethology began to include a much broader toolkit and conceptual framework, while still attempting to maintain the naturalistic focus on behaviour and evolution.

A particularly influential paper by Tinbergen (1963) helped broaden the focus of ethology by pointing out that questions of causal mechanism, development, evolution, and adaptive function were all critical ingredients in understanding behaviour. Indeed, his later work with students specifically incorporated comparative and causal mechanism research with the function of even seemingly trivial behaviour in the field. Adding a fifth area to Tinbergen's four, that of the experiential world of animals, helps connect ethological work to current research in neuroscience and psychology (Burghardt 1997). Currently, broader conceptions of developmental processes, perception, neuroscience, molecular genetics and phylogenetic analyzes, animal sociality, and a return to more field studies of behavioural function are now evident. In fact, behavioural ecology, an important pillar of current animal behaviour, can be viewed as merging the functional focus of Tinbergen's later work with both earlier basic ecology and the subsequent development of sociobiology and kin selection typified by

E. O. Wilson's *Sociobiology* (1975), the writings of William Hamilton (1964), and subsequent reassessments (e.g., Wilson & Wilson. 2007).

Behavioural Ecology

The current thriving field of behavioural ecology, with its own journals and societies, derives from many threads established in the nineteenth and early twentieth centuries. There are at least four approaches to using ecology for examining many aspects of behaviour. One is to observe animals in nature to derive hypotheses and then further test these on other groups of the same species. A second pathway involves taking information gained about one species in nature and testing it on additional species. In this way, generalizations are possible, or it may be the case that new discoveries are made about different species responding to the same or similar environments. Third, the specific behaviour patterns of a species can be explored in one or more locations or habitats. Last, one can take discoveries from the laboratory and test them under field conditions as well as the reverse.

Some examples of these four approaches provide a better understanding of them. For example, one key ecological phenomenon is succession, whereby the plant and animal communities in a particular location change over time. A common pattern involves either logging or a fire destroying a forest habitat. It is then possible, through observations and trapping, to study what rodents and birds colonize the area as it regrows, taking several decades to attain the former forest plant communities.

Another approach is to assemble hypotheses about the life history traits of the animals in a particular location. Usually this is done on a species-specific basis. So, for example: What is the breeding season for different bird species? Do these species vary in terms of when, from spring through the summer, they engage in mating and nesting activities? Do some breed multiple times and others just once? Topics that are pertinent to these questions included spatial distribution patterns such as territoriality, clutch size and single or biparental care, dispersal, and migration. By following these particular species over a number of years it is possible to obtain a thorough picture of the habits of each and also to gain knowledge about variations in the individual species. These types of data are particularly pertinent now as climate change has affected breeding seasonality and migration patterns for a number of avian species. Another applied aspect of these types of investigations is built upon a knowledge of the food web for a particular community of plants and animals. If, for example, overhunting or disease eliminates a species from the local community what then happens to the other relationships in that location? Depending on feeding habits, elimination of a particular animal species may change predator-prey relations and alter the dynamics of the food web.

For the third set of studies, one observes specific behaviour patterns of an individual species or several species at the same times and locations. This sort of information is used to generate and test several types of hypotheses. Data may be gathered on diverse subjects; examples are foods consumed, nest locations, or aggressive interactions that could lead to mapping territories. Possible hypotheses generated would include those pertaining to different species consuming some of the same foods, a phenomenon called niche overlap, or determining whether certain tree types were favored by different bird species for nesting locations.

A final pathway for examining issues pertaining to behavioural ecology involves using both field and laboratory settings (Snowdon & Burghardt 2017). Phenomena recorded and studied in the laboratory setting can be tested under both semi-natural and field conditions. Or, behaviour observed in nature can be brought to the laboratory to test specific hypotheses under more controlled experimental settings. Exploring cues used for orientation by migrating birds provides an example where field observations indicate various lunar or solar cues are used, this can be tested in the laboratory with caged birds and artificial, manipulated cues (Emlen & Emlen 1966). In the opposite direction, chemical signals in rodents that influence the timing of sexual maturation and mating in house mice were explored extensively under semi-natural conditions with demonstrated effects on population reproduction and growth (Drickamer & Mikesic 1990).

Thus, behavioural ecology is a multi-faceted approach to understanding the actions of animals and their functions in nature, and has been greatly enhanced by the recent development of methods of tracking even tiny animals remotely in the field. By combining a variety of thought pathways to develop hypotheses and performing tests under both field and laboratory conditions, more complete explanations for behaviour emerge. Modern behavioural ecology, more so than early ethology, has focused attention on testing the adaptive functions of behaviour, building on the work of Tinbergen's aim of studying adaptive function. The focus on function was abetted by the advent of sociobiological theory and modern molecular genetics that allowed for studies of relatedness and genetic variability within and between populations. Historically, however, this approach has been less interested in the underlying mechanisms and development of behaviour.

A hallmark of behavioural ecology is the development of models for various aspects of behavioural ecology, such as for example foraging behaviour, communication, and habitat selection (Krebs & Davies 1989; Patricelli & Hebets 2016). A great deal of this research has led to comparative analyses that affect both our basic understanding of principles of animal ecology and aid efforts, in recent decades, for conservation of endangered species. A key outcome measure for such studies should be fitness as measured by both production of progeny and their survival. To date, it is too often the case that the extra effort needed to truly assess these two outcome measures falls short of what is needed for a complete judgement regarding theories developed for topics like optimal foraging and mate choice. Including true fitness outcomes should become more prevalent in behavioural ecology.

Comparative Psychology

So where does this leave comparative psychology? By the end of the nineteenth century, animal behaviour was being studied in naturalistic contexts by biologists, including some experiments, crude by modern standards as they were. But counter currents, inspired by Darwin, especially his books on sexual selection and human evolution, behaviour, and emotions (Darwin 1871, 1872; Burghardt 2009), and ratcheted up by Romanes, were galvanizing scholars in areas outside biology in psychology, sociology, anthropology, philosophy, religion, ethics, and economics. Darwin famously wrote at the end of the of *On the Origin of Species* that in the future research "far more important" than those recounted in his book would be forthcoming. "Psychology will be based on a new foundation, that of the necessary acquirement of each mental power and capacity by gradation. Light will be shown on the origin of man and his history" (Darwin 1859: 488). Romanes, to whom Darwin entrusted his behaviour notebooks, entered the fray. Although he built his career initially as a careful student of the nervous system and simple behaviours, such as righting, in marine invertebrates, as for example echinoderms, he refashioned himself as a student of animal intelligence and the mental evolution of animals and people (e.g., Romanes 1883). He used largely anecdotal evidence to construct trees of the evolution of cognition, including perception, and mentality both across species as well as in the ontogeny of human infants. Darwin's program mandated that the differences among species, including humans from other animals, were grounded on continua, including intelligence, instinct, reproduction, fighting, sociality, and morality. His and Romanes's evidence, however, often rested upon anthropomorphic interpretations of animal abilities based on uncritical anecdotes in a time before film and audio records were readily available.

Presented in this light, the view that the main goal of comparative psychology is to uncover and assess the roots of our own behaviour in other species seems obvious. Certainly, this was the interest of many psychologists who began working on animal behaviour in the last decade of the nineteenth century. Remember that the first formal experimental laboratories in psychology did not exist until Wundt established one in 1875 at the University of Leipzig and William James did so the same year at Harvard University (Harper 1950). The first students and published research from these labs were several years in the future, just about the time Darwin's and Romanes's books were published. The work of these laboratories basically built on the sensory physiology and perceptual discrimination work carried out by physiologists. With the advent of Darwinism, new and exciting vistas seemed to beckon. James's (1890) *Principles of Psychology*, perhaps still the most influential and important book on psychology published in the United States, was based on evolutionary ideas, with prescient chapters on instinct, perception, the brain, emotion, thinking, formation of ideas, and consciousness among many other topics. It is thus understandable that psychologists would take over from the founders of comparative psychology, Romanes and Lloyd Morgan, the broader remit of incorporating an anthropocentric focus in what was, and still is, a largely human behaviour, brain, and mentality focused field.

For our purposes, in giving a capsule history of change and stasis in comparative psychology, we compare major overviews of the field rather than major figures and specific theories. The most recent is the two-volume, 80-chapter comprehensive *APA Handbook of Comparative Psychology* edited by three former editors of the *Journal of Comparative Psychology* (JCP) and two other prominent contributors to avian cognition and animal learning (Call et al., 2017). We begin, however, with the massive three-volume *Comparative Psychology: A Comprehensive Treatise* by Warden, Jenkins, and Warner (1935, 1936, 1940) published over several years, covering the period prior to World War II, and little known today.

The first volume is titled *Principles and Methods,* and includes a 52-page history that, even in retrospect, is quite accurate as well as more comprehensive than many more recent short treatments. All but 2 pages focus on Darwin and beyond. They divide the period into an initial anecdotal period where even Darwin was criticized, though gently compared to Romanes, followed by an experimental period. Lubbock and Morgan mark the break from the anecdotal period to the experimental one. Jacques Loeb's tropism research, Thorndike on instrumental conditioning, Pavlov on 'classical' conditioning, Small and Watson on mazes, Yerkes on learning and discrimination, are all viewed as initiating critical breakthroughs from anecdote and crude anthropomorphism. However, in raising the profile and importance of experimentation, the authors seemed to also devalue naturalistic observation and field studies with rare exceptions, in spite of their writing:

> At best the anecdotal material served only as a temporary purpose in connection with the controversy over the mental evolution of man. Furthermore, the anecdotalist movement was a positive evil in so far as its influence tended to retard scientific investigation of the behavior of the higher animals. The observation of the naturalist and the more careful studies of anatomist and physiologist, in so far as their findings were relevant, represent the more permanent contributions of the period to comparative psychology.
>
> *(Warden et al. 1935: 19)*

Later they also note that "Field observation must always hold a place of honor in the biological sciences and particularly so in comparative psychology" (ibid.: 30).

The discussion of the experimental period devoted much space to the ingenious methods developed by comparative psychologists to study the behaviour of both invertebrates and vertebrates, especially mammals. They point out that in terms of theoretical issues, following James in 1890, where and how consciousness emerged in evolution, and how to measure it, along with other subjective traits were major concerns. Loeb's mechanistic tropism theory sought to explain virtually all of human behaviour in simplistic terms by including associations (Loeb 1918). Others such as Morgan and Yerkes tried to develop theories of psychic levels, an approach that Schneirla and his school continued supporting for decades (e.g., Aronson, et al. 1970). Laboratory experimentation became the main touchstone for CP, not fieldwork, especially studies of problem solving, maze learning, and sensory abilities and discrimination. Interestingly, even when, in 1936, Watson had been out of comparative research for about 15 years, the authors could still state that "In variety, amount, and importance of experimental contribution during the past quarter century, Watson ranks second to none among the psychological group" (Warden et al. 1936: 40). He clearly is a person whose works steered the field greatly and was esteemed. Yet Watson, along with Kuo and others, basically opposed and ridiculed studies involving inherited natural motivational and behavioural systems (e.g., instincts), which are now becoming increasingly influential in neuroscience circles (Anderson 2016; Burghardt & Bowers 2017; special 2019 issue of *Behavioural Processes* on the contributions of William Timberlake and behaviour systems approaches; Krakauer et al., 2017).

Warden et al. (1936: 48–49), however, concluded that it was "extremely unfortunate that the speculative spirit [meaning the search for "a picture of the subjective life of infra-human forms"] should have held so dominant a place in in the earlier decades." Indeed, they viewed the 'objective movement' as essential to freeing CP from subjectivism and anthropocentrism and that CP must "develop a content independent of human reference in the same sense that zoology is independent of human morphology and physiology" (ibid.: 54). And to a great extent the three volumes of the treatise tried to do just that. The rest of the volume on *Principles and Methods* grounded CP in the evolutionary, developmental, and physiological biology of the day, including a focus on experimental methods of testing sensory abilities, motivation, and intelligence. These three areas are indeed the primary legacy of CP from that era. There are no entries in the index of that volume for sexual selection or social behaviour!

That is not the case with the other two volumes in the series, however. Volume two, devoted to plants and invertebrates, is by far the longest, at over 1000 pages with about 5000 references. It is a most detailed coverage with, however, very little actually written by psychologists. It is, we suggest, still a valuable source for the early literature on the behaviour of plants, single-celled organisms, and virtually all groups of invertebrates. The work of proto-ethologists such as Jakob von Uexküll is well-represented along with many other pioneers. Interestingly, in the light of articles bemoaning how the contributions of perhaps the first Black animal behaviourist, C. H. Turner, have been ignored (Dona & Chitka 2020), the arthropod chapter alone includes citations to 29 papers by Turner! Turner did focus on individual differences and cognitive abilities that were not that congruent with the times. Still, later comprehensive surveys ignored his contributions almost entirely.

The third volume on vertebrates has comprehensive coverage of fish, amphibians, reptiles, birds, mammals other than primates. The fewest citations are in the reptile chapter, confirming their great neglect in CP and biology and behaviour generally (Doody, Burghardt, & Dinets 2013; Burghardt 2021). Sexual selection is not mentioned and social behaviour is listed under group behaviour with but several mentions. This volume does contain contributions by more psychologists than the other volumes and is a fascinating glimpse at now often forgotten methods, questions, and findings. In fact, the entire series contains about 400 illustrations of the leading personages, apparatus, and behaviour that really deserve some downtime exploring.

It is also important to note that social behaviour was not totally ignored by comparative psychologists. The seminal *Handbook of Social Psychology* edited by Murchison (1935) included lengthy chapters on social behaviour in bacteria, plants, insects, birds, herd mammals, non-human primates, as well as chapters on animal aggregations by W. C. Allee and dominance hierarchies by Schjelderup-Ebbe, foundational researchers on these topics. Ecological factors, including numerous animal examples, were admirably covered by Victor Shelford, a leading ecologist. This collection is remarkable in that these subjects were covered in 10 chapters in a 1200-page book with only 21 chapters! One wonders what the shape and relevance of current social psychology would be today if the current largely experimental computer laboratory-oriented and survey-infused social psychology popular today had followed the leads in this book in terms of studying actual human social behaviour in natural settings from an evolutionary perspective.

One can thus appreciate that characterizing comparative psychology is difficult historically as it has incorporated a variety of research questions, theory, and methods. In 1987, upon the publication of the hundredth volume of the JCP, the then editor, behaviour geneticist Jerry Hirsch, brought together many prominent people in the field and asked for their reflections. They are useful to reread, but are given capsule summaries in Burghardt (2013), a later editor of the JCP who found several themes. The major ones involved whether CP should be directed at understanding human behaviour, focus on the species being studied, or search for general principles. The role of comparison is another issue; that is, how explicitly *comparative* does a study need to be? How do we best apply findings cross species; that is, the role of both similarities and differences?

Today much misunderstanding of CP still exists both among psychologists but also among biologists who are wary of psychology in general and some of the excesses of evolutionary psychology (Burghardt 2013). Some see CP as exclusively focused on laboratory studies, or behaviouristic studies of animals learning, while others seem to identify it as primarily a field of comparative cognition focusing on non-human primates with the occasional dog, parrot, or cetacean thrown in. All these are false and belied by the history, though all represent some major emphases over the years.

Donald Dewsbury, not only an active researcher in rodent behaviour, but one who devoted much of his career to the understanding of CP and its history (Dewsbury 1984a, b), tried to exclude most behaviouristic learning studies of animals from CP proper as being too focused on general principles and thus not truly comparative. Conversely, he also tried to make the case that even behaviourists such as John B. Watson did fieldwork that appeared very ethological and in the Tinbergen mold. These views came under some criticism in the 1987 reappraisal. However, he and Boakes (1984) wrote perhaps the most detailed monograph-length historical reviews of comparative psychology and no more recent ones seem to exist.

Thirty plus years on from his seminal works, however, Dewsbury wrote an updated brief historical overview of CP for the *APA Handbook of Comparative Psychology*. Rather than trying to define and characterize the field in any definitive manner, he decided to view the field as one with recurring themes that waxed and waned over the decades as "various forces" led to some themes becoming dormant and then regaining prominence, as well as the field moving "into areas not previously anticipated" (Dewsbury 2017: 17). Dewsbury identified six major themes and the questions comparative psychologists sought to answer both before and after World War II (with most emphasis on the post-WW II period). His six areas are *Evolutionary comparative psychology*, *Developmental comparative psychology, Behaviouristic comparative psychology, Physiological comparative psychology, Ethological comparative psychology,* and *Cognitive comparative psychology*. Behavioural ecology is largely ignored and applied issues, such as are involved in captive animal welfare, environmental issues such as pollution and climate change, and conservation are barely mentioned, but this lack was also true in the 1987 reassessment. Yet these areas may include some of the most important problems CP should address given that psychologists have a long history of experimental and quantitative sophistication that ethology and ecology, being more focused on description and natural history, largely lacked in the early decades of each field. Dewsbury (2017) offers a succinct survey of his six themes and they also can be compared to the four aims of ethology described by Tinbergen (1963) in his charge to the field of ethology. Frans de Waal (2016) wrote a fascinating popular historical recounting of ethology and CP from a personal primate-centric focus.

Before we move to the 2017 treatise on CP, we also highly recommend the excellent compact CP handbook edited by Greenberg and Haraway (1998), which contains useful historical contributions including capsule biographies of leading personages (also present in Dewsbury 1984a) and international and philosophical perspectives. The 100 chapters cover all the major topics and major taxa in authoritative brief chapters by leading experts, and show how the ultimate goals put forth by Warden et al., were finally bearing fruition. The most comprehensive recent attempt, however is the aforementioned two-volume massive compilation published by the American Psychological Association (Call et al. 2017). These volumes show continuity with earlier work in comparative psychology, but also more established links with ethology, neuroscience, and cognitive psychology.

The first volume, *Basic Concepts, Methods, Neural Substrate, and Behaviour*, contains 45 chapters. In addition to history, chapters cover diverse methods, including fieldwork, experimental methods, apparatus, networks and statistics, individual differences, personality, and comparative phylogenetic methods. Other chapters tackle adaptation and evolution, genes, hormones, and development as well as comparative neuroanatomy, instinct, behaviour systems, emotion, birdsong, laterality, biological rhythms, processing of spatial and temporal information, and neural networks. Finally, 16 chapters cover major behavioural systems including thermoregulation and energetics, communication, play, maternal and paternal care, courtship and mating, feeding, anti-predator behaviour, fear ecology, fighting, conflict resolution, friendships, and cooperation.

The second volume, *Perception, Learning, and Cognition* in 35 chapters covers more traditional topics in experimental comparative psychology, but all with new twists and new directions. The first part tackles the major sensory systems, psychophysics, visual illusions and picture recognition, working and episodic memory, and attention. The second part has chapters covering basic conditioning, evolution, decision making, optimality, and social and cultural learning, while the third part, visits many aspects of comparative cognition, problem solving, creativity, reasoning and self-recognition, ending with a final chapter on animal welfare science. In Volume 2 the behavioural and cognitive areas are parsed into more focused units than are the chapters on the more functional behaviour topics in Volume 1. The authors of these 80 chapters identify not only as psychologists, but also as neuroscientists, physiologists, behavioural ecologists, and ethologists.

We close by looking at the first chapter in Volume 1, What is Comparative Psychology? It clearly echoes what has been noted above, that CP "is a diverse field with strong multidisciplinary connections. … draws on and contributes to many areas of the natural and social sciences … as well as many areas of biology and even the humanities and religion" (Call et al. 2017: 31). In fact, seen in this way, CP overlaps greatly with much of ethology and behavioural ecology. Three overlapping circles would make a Venn diagram, but actually what to put in each circle for the fields would now be difficult to discern, other than relative emphases, and what departments or institutions one works in, or the more specialized journals where scholars publish when not writing for general multidisciplinary journals. While this is very encouraging, it is also important to note that some laboratories are more likely to recognize the value or work done in some related fields than others, a product of the increasing specialization as fields grow. Relevant papers should be sought out wherever available, and more of this should occur whether the scientist identifies primarily as a psychologist, ethologist, ecologist, geneticist, anthropologist, neuroscientist, evolutionary biologist, or taxon specialist be it entomologist, ichthyologist, ornithologist, herpetologist, primatologist, etc.

What will the future of comparative psychology look like? For some (e.g., Crystal, 2021) studies of comparative cognition from an anthropocentric orientation are the proper focus, and this may be how the field develops going forward. But this differs from how we hope comparative psychology might develop and so we opt to provide a few sentences from our respective vantage points and perspective. Methods of gaining details of animal movements, migration, behaviour, mating, parental care, social structure, foraging, paternity, genetic relatedness, and habitat use in the field are growing rapidly and will allow more detailed data that formerly were only possible in captive settings if at all. Experimentation, including natural events such as before and after catastrophic events (volcanic eruptions, fires, floods, droughts, logging, etc.,) or more slow acting events such as invasive species and climate change will help us untangle the roles of genetic and cultural inheritance, behavioural plasticity, and perceptual, cognitive, affective, and social processes. Zoos and field settings can help in understanding what psychological, physiological, and behavioural factors are most critical in conservation biology and rehabilitation and reintroduction of endangered species as well as all the domesticated animals we keep by the millions along with all the companion animals, both domesticated and exotic, we treasure but may be underestimating in many ways. Consider the enormous growth of research findings on dogs in recent years. Similarly, animals we value less, varmints and disease-bearing species may have secrets to tell with both applied and intellectual consequences. Flies, sharks, crocodiles, sea urchins, and many other non-traditional species should be explored and break away from the species limitation so prevalent just a few decades ago when rats and pigeons were the primary species of choice for comparative psychologists. Finally, the debates over instinct and learning, nature and nurture, while abating, still pose the question of integrating ontogenetic and evolutionary processes. The field of evo-devo is a promising development, but a behaviour systems approach that moves beyond the misunderstood concept of instinct offers, in our view, the most viable integrative approach uniting psychology, ethology, ecology, and evolution in a field that may be labeled ethological psychology, comparative evolutionary psychology, or in some other way bring together in an effective manner the disparate threads that are essential for weaving a tapestry that truly covers the lives of all animals, humans included.

Conclusions

We have taken a somewhat different approach to examining the history of CP and encourage students as well as seasoned researchers to revisit classic studies in their fields of interest as well at their general fields (c.f., Burghardt 2020). While many studies may be available on the internet, books of organized readings can be particularly useful and convenient. A broadly based selection is found in Houck and Drickamer (1996). Classic readings in comparative psychology can be found in Dewsbury (1984b), while important classics in comparative ethology are available in Burghardt (1985) and Klopfer and Hailman (1972a, b). One of the messages from comparative psychology is that many of the leading contributors viewed biology as a critical area in which comparative psychology should be embedded. The seminal volume, *Psychologies of 1925* (Murchison 1926) is largely devoted to chapters by leaders in behavioural psychology including Watson, Dunlap, Kőhler, Hunter, McDougall, and Bentley. The connections with biology were frequently mentioned. Watson, for example, claimed that "No one should attempt to make studies upon the infant" without "considerable training in physiology and in animal psychology" (Watson 1926: 15). But William McDougall (1926: 281), points out that Watson's biology, by completely discrediting any instincts and inherited mental traits in humans, is as "magnificent" in his "defiance" of science as was William Jennings Bryan's "of the evidence for human evolution" in the Scopes trial. McDougall's chapter was one of the first in psychology to discuss robots! Wolfgang Kőhler in his chapter (Kőhler 1926) records that a chimpanzee who knew how to use sticks as tools, and finding himself without one, after a considerable period suddenly broke off a branch from a tree and made a tool to obtain the reward, and this decades before Jane Goodall's work in the field! In other words, there are gems in the early writings, if only we care to look. There are also volumes of the collected papers of important figures such as B. F. Skinner, Clark Hull, Neal Miller, Konrad Lorenz, Niko Tinbergen, Frank Beach, Desmond Morris, Erich von Holst, and others. The autobiographical chapters in the series, *A History of Psychology in Autobiography*, started by Murchison in 1930 and continuing into the twenty-first century, has, especially in the early volumes from the 1930s, excellent perspectives by eminent early comparative psychologists. For modern leaders in animal behaviour, including psychologists, the volumes edited by Dewsbury (1985) and Drickamer and Dewsbury (2010) are especially recommended as they involve reflections by more recent figures, whose essays discuss their experiences as well as recent developments and controversies. But nothing really replaces physically inspecting original books and journals in libraries or in today's online reproductions, which more intimately and emotionally allow us to be situated in the past and reflect on the history of our attempts to understand the behaviour of life on earth and the struggles to situate ourselves within this ancient and still ongoing history.

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2

BEHAVIOURISM

Past and present

Gonzalo P. Urcelay and Joaquín M. Alfei

In his 1913 manifesto, Watson (1913) proposed that "psychology as the behaviourist views it is a purely objective experimental branch of natural science. Its theoretical goal is the prediction and control of behaviour". These statements represented a reaction to mainstream psychology that focused on mental states as the construct of study, and introspection as the technique to assess them. What Watson tried to achieve in his manifesto, was a discipline of enquiry that was aligned with the principles of Darwin's evolutionary theory and the methods of the natural sciences - rooted in positivism and making no distinction between humans and other animals. Many at the time considered that psychology should use observation as a method of data collection and avoid making inferences about mental states which can only be inferred from verbal behaviour. A larger goal of Watson's manifesto was to proclaim behaviourism as the mainstream discipline in psychology. Textbooks in the history of psychology tend to devote one or two chapters to "behaviourism" and swiftly move on to argue that the fall of behaviourism was triggered by the "cognitive revolution". In this chapter, we shall argue that this misrepresents the goals and breadth of behaviourism (as stated by Watson and other [neo] behaviourists), by confusing some of behaviourists' positions (i.e., radical behaviourism) and distinguishing behavioural from cognitive psychology. First, we will make a brief historical revision. Then, we shall review developments in animal learning that strongly suggest that the science of behaviourism is in line with concepts that have been taken as unique evidence for the cognitive sciences. The last part of this chapter describes recent developments which collectively suggest that behaviourism is rampant and has had a strong impact in disparate fields including, of course, comparative cognition.

Contemporary to Watson, Pavlov (1927) and Thorndike (1911) were also interested in the study of behaviour, in particular learning processes. Findings in Pavlov's laboratory revealed that dogs started salivating to the sight of foods, and bolstered the case for stimulus (sight of food) response (salivation), or S-R learning. Following pairings of the sight of food (conditioned stimulus; CS) and the nutritive effects of the food (unconditioned stimulus; US) the CS elicits salivation (conditioned response; CR). Similarly, Thorndike, who was training cats to escape puzzle boxes, observed that cats' latencies to escape became faster with training. He also appealed to a stimulus-response (S-R) mechanism to explain this. He proposed that the association between environmental stimuli and a specific response were "stamped in" by the reward, in what is known as the "law of effect". The prevalence of an S-R mechanism to explain all forms of learning was challenged by a clever study in Jerzy Konorski's lab, where the first distinction between Pavlovian and instrumental learning was made. Miller and Konorski (1928) conducted an experiment in which dogs were presented with a discriminative stimulus and their legs were simultaneously flexed by the experimenter. This compound of stimulation (external discriminative stimulus plus leg flexion) was followed by the

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presentation of food in the dog's mouth. Following numerous pairings of the compound with the food, they observed that the dog would flex the leg upon sensing the stimulus, a finding that was at odds with Pavlov's notion of S-R, because this would have anticipated that salivation (rather than leg flexion) should have been observed upon presentation of the stimulus. They concluded that, although sharing some similarities, classical (or Type 1) and instrumental (or Type 2) conditioning procedures were operationally different.

Although Watson's goal was that of a discipline devoid of any internal constructs, it soon became obvious that animal learning was much richer than what was captured by S-R theories, and hence that this account was insufficient to explain the different phenomena under observation. This challenge was taken by Tolman and Hull, among others, who appealed to the notion of "intervening variables" (variables within the organism such as cognitions and motivation) to explain phenomena that were not explained by a S-R mechanism. Tolman (1922) proposed "a new formula for behaviourism" with two goals: the first one was theoretical, bringing under a single rubric of behaviourism different methods, and the second was practical – he wanted behaviourism to provide an adequate treatment of problems of motivation and purpose, but with the use of behavioural methods. Importantly, Tolman's ideas are consistent with what later became known as "cognitive psychology". One striking finding that supported Tolman's proposal was that of "latent learning" (Tolman & Honzik, 1930). In the experiment, rats had to go through a complex maze and were allocated to three groups based on what they experienced at the end of the maze. Two groups are relevant here. One group consistently received a reward on each trial, and the number of errors in this group decreased through the 17 days of training. A second group, however, received no rewards during the first 10 days of training, and got their first rewarded trial on day 11. On day 12, this group performed numerically better than the group which obtained rewards at the end of every single trial. This finding suggested that (a) animals could learn in the absence of reinforcement, and (b) this learning was not reflected in performance until rewards were presented. Thus, they concluded that reinforcement influences performance rather than learning.

The notion that intervening variables matter was also taken by Clark Hull (1943) who returned to Watson's S-R psychology, but argued that it was drive reduction (rather than affective evaluation) that made learning benefit from reinforcement. He developed a formal theory of learning that captured these constructs and instantiated them in his Mathematico-Deductive theory of learning. In contrast with these views which accepted intervening variables, Burrhus F. Skinner (1974) developed "Radical Behaviourism", a strong version of behaviourism which assumes that "intervening variables" are unimportant and therefore all that matters are environmental determinants of instrumental behaviour. Skinner was a highly prolific (and parsimonious) thinker who (along with students he trained) went on to develop radical behaviourism as a separate field of study. He argued strongly against cognitive psychology and any attempt at explaining behaviour in terms of "internal" constructs, proposing that all forms of behaviour (including language) could be explained with (non-representational) S-R links. In summary, behaviourism started as an independent discipline with the goal of using behaviour as the dependent variable (rather than introspection) and avoiding resorting to internal constructs such as consciousness and internal mental states. This led to different ideas, all of which emphasized the importance of using behaviour as the unit of analysis, but differed in whether internal constructs should be used to explain behaviour.

These differences persist until today, however we shall underscore the observation of "blocking" by Kamin (1968) as a turning point in the development of theories of learning, which was captured (and still is as argued below) as evidence for internal constructs such as that of "surprise". That is, whilst the cognitive revolution was in its zeitgeist, Kamin conducted an experiment in which two groups of rats received pairings of a compound made of a tone and a light, which was followed by a mild shock. For one of these groups, the "blocking" group, the light had previously been trained as a strong predictor of the shock. Kamin observed little learning about the tone-shock relationship in the group that received prior training of the light. That is, animals in the blocking group that had previously experienced light-shock pairings failed to show fear to the tone during testing. Kamin interpreted these results in terms of "surprise". He argued that for animals in the blocking group, the shock was not surprising during the second phase because it was already predicted by the light, bolstering the notion of "prediction error" as a condition for learning to occur.

The notion of prediction error was adopted by the well-known Rescorla-Wagner model (Rescorla & Wagner, 1972; hereafter, R-W), one of behaviourism's biggest successes. Like its predecessors, the R-W model assumes that learning during a given trial is determined by the difference between what the animal expects, and what it experiences. Before any training, the expectation is zero and therefore the change in associative strength is large. As training proceeds, what is expected becomes similar to what is experienced, and learning plateaus. What distinguishes the R-W model from its predecessors is that the expectation is based on all stimuli present on a given trial. Applied to the blocking example mentioned above, during the first trial in which the light and tone compound was followed by shock, the shock was fully expected based on the previous light-shock pairings, and therefore little learning to the tone is anticipated, which is in line with the outcome of the experiment. Blocking, together with overshadowing, relative validity and over expectation, are known as "cue competition" phenomena and are captured by the R-W model. Although some have also observed facilitation between CSs trained together, cue competition phenomena are a gold standard that all contemporary models predict (Urcelay, 2017). The notion of prediction error suggests that expectations play a strong role in learning, and additional findings bolstered the case that animals can indeed represent events in their environment following learning, and that these representations not only command further learning but also performance at test. In the next section, we will briefly describe three findings that led researchers to conclude that animals do indeed use representations of past events to guide their behaviour in the laboratory. These findings are entirely consistent with some of the claims that made cognitive psychology an independent field of research, and thus place behaviourism at a similar level of complexity as cognitive psychology. In fact, by the early 1980s, learning theorists investigating behaviour were already speaking about "associative representations" (Dickinson, 1980), and we will discuss some of this evidence next.

Associative (cognitive?) representations

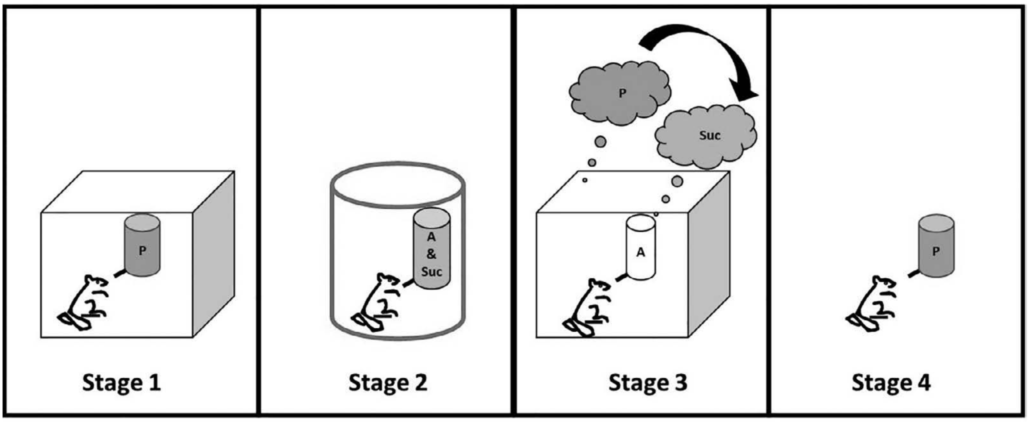
We will describe three phenomena that led scientists to conclude that animals can represent events previously experienced, integrate them, and use this information to guide their behaviour. The first of such phenomena were revealed by a technique known as "outcome devaluation". This was used in an experiment conducted by Holland and Straub (1979). Two groups of rats experienced pairings of a noise and food pellets. After four sessions, rats learned that the noise was a predictor of pellets, and therefore searched for pellets in the magazine when the noise was presented. In a second phase, rats in the critical group were given the opportunity to eat food pellets and this was followed by an injection of Lithium Chloride (LiCl), which made them ill. Rats in the control group also received LiCl but in the absence of the food. During this second stage, rats in the experimental group learned that food was followed by poisoning and therefore rejected eating the food after a few pairings. At issue was whether rats would approach the magazine in a final test, when they heard the noise again, but in the absence of food. If rats could integrate the information learned during the two phases, then at test rats in the experimental group should approach the magazine when hearing the noise less than rats in the control group, because the noise should retrieve a representation of the (now devalued) food pellets, and this is what they observed. A similar observation was done by Adams and Dickinson (1981) but using an instrumental procedure. They trained rats to press a lever in order to earn a total of 50 reinforcers. In addition, rats also experienced sessions in which they received non-contingent reinforcers of a second kind; these reinforcers were given in the absence of any lever presses. Following training, rats were allowed to eat either the reinforcers that they earned during the instrumental sessions (Group Contingent) or the pellets that were given non-contingently (Group Non-Contingent) and these were followed by LiCl injections. Presumably, the illness produced by the injections should devalue the reinforcers that followed a lever press in Group Contingent, but not in Group Non-Contingent. Following three cycles of outcome devaluation training, all rats were tested in the chambers with the lever presented, but in the absence of any reinforcers during the test session (i.e., in extinction). This allowed the researchers to assess whether rats could represent the value of the pellets that they previously earned during instrumental training. Their results paralleled those of Holland and Straub, in that rats in Group Contingent displayed less lever presses at test than rats in Group Non-Contingent. Subsequent test sessions where lever presses did result in presentations of the reinforcers showed that all rats had learned the aversion to the reinforcers. In summary, these experiments show in Pavlovian and instrumental training scenarios that both of these forms of learning show sensitivity to the value of the outcomes, thus suggesting that in these forms of associative learning animals represent the identity and value of the outcomes, a finding which is consistent with the cognitive account.

In subsequent experiments using Pavlovian learning, Holland assessed whether animals could learn about events that, rather than being presented during the learning session, were associatively activated (i.e., imagined) by virtue of the presentation of another stimulus which was previously associated with the target stimulus (see Holland 1990 for a review). The experiments described above suggested that following Pavlovian conditioning, the CS is able to activate a representation of the US, so that when the US is devalued, the CS evokes little CR. Holland asked whether the representation of the US that is activated by the CS involves those aspects of the US involved in the production of the CR, or whether the CS is able to activate perceptual properties of the US. In order to answer this question, he exploited the taste reactivity test (TRT) developed by Grill and Norgren (1978). The TRT assesses the hedonic reactions evoked by USs by assessing the pattern of orofacial responses evoked by positive, neutral, and negative flavours. That is, the authors observed that intra-oral infusion of sweet flavours resulted in "ingestive" reactions, such as tongue protrusions, rhythmic mouth movements, and paw licking. Conversely, infusions of bitter flavours produce "aversive" reactions such as gaping, head shaking, and flailing of the forelimbs. Holland made use of this technique to assess whether the US evoked representation involved perceptual aspects of the US (i.e., taste processing). He paired two tone CSs with peppermint and wintergreen-flavoured sucrose solutions (USs). During this stage, flavoured sucrose solutions evoked ingestive reactions, as expected. In a second stage, he paired one (but not the alternative) of the flavoured sucrose solutions with LiCl in order to devalue one of the flavoured solutions (as in previous experiments). At test, he presented the tone CSs whilst rats were consuming a plain sucrose solution (with no flavours). Critically, he assessed ingestive and aversive reactions whilst the two tones were presented. Consistent with the notion that CS-US pairings endowed the CSs with the ability to evoke sensory-specific US responses, he observed that the tone paired with the food which had undergone devaluation now evoked aversive reactions, despite the fact that the flavour was not present at test. In other words, the rats displayed aversive responses to the absent flavour.

Having observed that following CS-US pairings the CS now was able to evoke sensory-specific responses of the US, even when the US was absent, Holland set out to assess whether these evoked (i.e., imagined) sensory-specific representations could enter into associations with other USs. He asked whether animals could learn about an imagined event, that rather than being presented was evoked by virtue of the presentation of an associated stimulus. During a first stage, rats experienced pairings of two tone CSs with two flavoured foods as US (as in previous experiments). These pairings should endow the two CSs with the ability to evoke sensory-specific representations of the flavoured USs. In a second stage, he paired one of the tones CSs with LiCl. At issue was whether the sensory-specific representation of the US which were evoked by the tone CS would enter into an association with illness induced by LiCl. He assessed this by giving rats at test the possibility of consuming both foods. He observed lower consumption of the food whose tone was paired with LiCl. A flavour that was evoked by presentation of the tone and paired with LiCl now tasted bad, revealing learning about an absent (but associatively activated) event (Holland, 1981). The notion that humans and other animals can learn about absent events and integrate this information during conditioned responding has now been confirmed in numerous studies using different procedures under the label of retrospective revaluation (not covered here, see Miller & Witnauer, 2016 for a review).

Having established that rats can learn about an event that is absent (but associatively activated), we will now describe an ingenious experiment which suggests that rats are capable of learning about two events which are absent (but associatively activated – or imagined) during the learning episode. This experiment was conducted by Dwyer and colleagues (Dwyer et al., 1998), and involved four stages (Figure 2.1). In Stage 1 rats drank a peppermint flavoured solution in a distinctive Context 1. During Stage 2, rats drank almond-sucrose solution in Context 2 (Contexts 1 and 2 were discriminated by the animals and different from their home cages). In Stage 3, the researchers then allowed the rats in the experimental group to drink a pure almond solution in Context 1. At this stage Context 1 should have activated the peppermint representation, while the almond solution should have activated the sucrose representation, causing a peppermint–sucrose association to be formed. If rats could associate these two activated representations, this should enhance the attractiveness of the

A) Experimental Group



B) Control Group

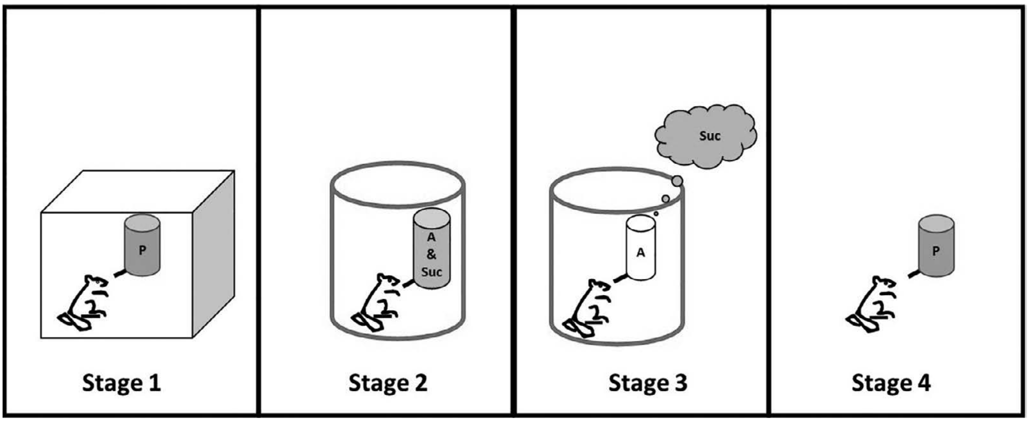


Figure 2.1 Panel A shows the treatments given to rats in the Experimental Group in the Dwyer Experiment. Note that the representations of Peppermint and Sucrose are evoked and associated during Stage 3. Panel B shows the treatment given to rats in the Control Group, where there was no opportunity to associate the two evoked representations during Stage 3, because rats were placed in the same context as in Stage 2. Animals in the Experimental Group consumed more Peppermint during Stage 4 than those in the Control Group.

peppermint. They compared during Stage 4 the consumption of peppermint with a control group that was equally treated, except that during Stage 3 this group of rats drank almond in Context 2, which should not have activated a representation of peppermint. In agreement with this prediction, during Stage 4 the experimental group drank more peppermint when tested in a third context than a control group. The authors concluded that during the Stage 3, animals in the experimental group activated a representation of each absent stimulus of the pair and learned the relation between these representations leading to increased preference for peppermint at test.

The examples mentioned above are only a few of many examples (see Savastano & Miller, 1998 for examples of encoding and integration of temporal relationships) in which carefully designed experiments conducted with the tools developed by the behaviouristic tradition revealed flexible use of different learning experiences. Moreover, they led scientists to conclude that the humble rat is capable not only of learning from experienced events, but also from events that were associatively activated, and deploying this information onto behaviour in a manner which is consistent with the basic ideas that were put forward during the cognitive revolution. For example, in his foundational book *Cognitive Psychology*, Neisser (1967, p. 4) stated that "*the term 'cognition'* (his emphasis) *refers to all the processes by which the sensory input is transformed, reduced, elaborated, stored, recovered, and used. It is concerned with these processes even when they operate in the absence of relevant stimulation, as in images and hallucinations*". Of course, this provocative definition challenged some behaviouristic conceptions back in 1967. We believe that today behaviourism is alive and thriving as it broadens its areas of influence and illuminates diverse areas of research. In the next section, we look at the influence of the behaviouristic tradition on contemporary research problems that span different areas, and different levels of analysis.

Behaviourism today

When and how learning occurs, how organisms forget over time, and how information from one situation can be used in similar or dissimilar situations represent just a few broad examples of the different aspects of behaviour and cognition that have been examined in a century of behaviourism. Undoubtedly, behavioural research in the lab has inspired a wide variety of research programmes beyond its own agenda. Here we will summarize a few examples of how behavioural research has provided key tools and guidance to contemporary fields of knowledge through precise hypotheses articulated in an a priori conceptual framework, careful task design, and collection of behavioural data.

Over the last three decades, the neurobiological study of learning and memory has progressed dramatically, fuelled in part by the availability of new technologies such as gene knockouts, multi-unit recordings, human and animal brain imaging, and optogenetics (which enables the manipulation of selective populations of neurones to assess their causal role in behaviour). Breakthrough discoveries in neuroscience have been supported by behavioural insights. A fundamental example is the discovery that midbrain dopaminergic neurons behave in a manner that is entirely consistent with associative theory: early in Pavlovian training, these neurons exhibit a strong phasic response to an unexpected reward, but as training proceeds, this response transfers back to the cue which predicts the reward occurrence (Schultz, 2016).

Prediction error (PE) is a key concept that lies at the heart of most current theories of associative learning, connectionist modelling and reinforcement learning, either by controlling changes in associative strength (Rescorla & Wagner, 1972) or associability (i.e., attention; Pearce & Hall, 1980). By definition, a PE during a learning episode is the difference between what is expected (based on previous learning) and what is experienced on a given trial. The PE provides a measure of the extent to which the occurrence of the outcome is unexpected or surprising and therefore specifies the extent to which learning is to occur. When the PE is zero, the CS provides an accurate representation of the predictive and causal structure of the environment. The concept of PE has attracted the attention of neuroscientists, stimulated by the finding that dopamine neurons appear to encode a general prediction error by responding to surprising, but not predicted, rewards in standard conditioning procedures such as blocking and extinction learning (e.g., Waelti, Dickinson, and Schultz, 2001). The concept has also provided the rationale and focus for several brain imaging studies of human learning (e.g., Corlett et al., 2004), and some have proposed that PEs represent a basic neural coding strategy (i.e., predictive coding; Rao & Ballard, 1999). In essence, this successful example illustrates how behavioural research on prediction error guides hypothesis-driven experimental design and ideas in neuroscience which explains the activity of key neural signals with precision. It is also important to note that it is widely accepted that the importance of such a concept (PE) is reflected by the fact that a variety of theories have incorporated it within their theoretical machinery, whereas its validity is endorsed by its extension from animal to human learning and by its role as productive concepts in bridging between psychology and neurobiology of learning and memory.

Another research area in which the notion of PE has been critical is concerned with the administration of an amnesic following memory retrieval. It has long been known that reactivated memories are susceptible to the effects of amnesics (Misanin, Miller, & Lewis, 1968). However, experiments from our and other laboratories have shed light on the conditions necessary for the amnesic to influence memory expression (Alfei et al., 2015; Monti et al., 2017). In these series of experiments using rodents as subjects and a Pavlovian fear memory task, we revealed how PE is the critical tool which renders a stable fear memory vulnerable to different manipulations that attenuate fear memory expression in a long-lasting way. These results have also been observed in humans (e.g., Sevenster, Beckers, & Kindt, 2013) and have been touted as a promising avenue for future (pre)clinical research oriented to treatment of emotional memory disorders, including post-traumatic stress disorder, anxiety-related disorders, and addiction (Beckers and Kindt, 2017).

In the domain of psychological (pre)clinical research and mental health, behavioural research has had far-reaching implications. A notable example that clinicians have incorporated are exposure-based strategies, originally generated in the domain of behavioural research. In the laboratory, the most widely used Pavlovian paradigms to study fear are contextual and cued fear conditioning. In the former case, a physical context (in rodent research usually the conditioning chamber) is paired with an aversive US (e.g., foot shock), whereas the latter involves a discrete cue, such as a tone, paired with shock. Critically, CRs (e.g., fear) can be reduced through repeated noncontingent presentations of the CS (e.g., tone) in the absence of the US (e.g., shock); the weakening of a CR because of CS-only presentations is called extinction learning (Bouton, 2002; Urcelay, 2012). Similarly, in clinical settings, exposure therapies in which a patient is (repeatedly) confronted with a fear-elicited stimulus or context in the absence of an aversive outcome are extensively used because it results in a decrease of CRs (Vervliet, Craske, and Hermans, 2013). Relatedly, note that lab and clinical researchers have been originally guided by the idea that extinction learning is a function of expectation discrepancy (i.e., prediction error) that occurs during the omission of the expected US, as is posited by the R-W model. The importance of this idea also lies in the fact that (pre)clinical research has systematically observed that exposure therapy might be enhanced by increasing the fear that patients initially experience during exposure and thus the discrepancy between the expectancy that something bad will occur and the fact that nothing bad occurs during therapy (Craske et al., 2014; see Urcelay, 2012 for ways to enhance extinction derived from basic research).

We now turn to review a few topics in comparative cognition where behaviourism has had a strong impact: social learning, learning of categories, and tool use. These examples illustrate how comparative psychologists have embraced the principles of learning derived from behavioural research as one of primary methodological tools to investigate animal cognition. Research on social learning in animals has revealed a rich variety of cases where different species – from insects, birds, fish, rodents, cetaceans, to primates - acquire biologically important information from observing the actions of others (Heyes & Galef, 1996). At the individual level, social learning helps naive individuals acquire information from more experienced individuals, resulting in behaviours that have positive outcomes (food) or result in avoidance of negative ones (predators). At the group level, social learning enables the transmission of behaviour between individuals and across generations, thus providing the opportunity for the establishment of traditions and other cultural phenomena. The adaptive value underlying social learning is that inexperienced individuals can learn to behave more efficiently by using social information from experienced individuals.

Over decades of research, different social learning phenomena have been described in many animal groups, and controversy has ensued regarding both the abilities of non-human animals and the mechanisms that underlie social learning (Heyes, 1994). For many years, it was widely believed that social learning in humans and other animals is dependent on a variety of genetically inherited mechanisms. However, this consensus has now evaporated, with many scientists arguing that most social learning phenomena can be supported by associative learning processes that encode information for long-term storage by forging excitatory and inhibitory links between event (stimuli and responses) representations (Heyes, 2018, Ch. 5). Some of the evidence supporting this claim comes from studies of social enhancement of food preferences in rats. These studies indicate that social enhancement of food preferences – one of the most well-researched and thoroughly examined examples of social learning in the field (Galef & Stein, 1985) – is subject to overshadowing and blocking (Ray, 1997), suggesting that these phenomena are mediated by prediction error mechanisms (see Heyes, 2012, for a review).

Organisms are exposed to a wide range of stimuli throughout their lives. In fact, no stimulus is ever experienced in the same way in the natural environment. Stimuli that vary in their physical properties can be grouped together and associated with a single response through categorization or concept learning. For example, a chair can be classified as part of a larger category that comprises chairs of all sizes, shapes, and styles. Chairs, in turn, can be thought of as examples of furniture or human-made objects. These higher-level categories are abstract, because the members of the category share fewer physical characteristics. People also form more abstract categories; for example, chairs and flowers also may be categorized in terms of a higher-level concept: artificial versus natural. Thus, humans are capable of learning regularities in the environment which are independent of the physical attributes of the stimuli, a capacity known as abstraction. Critically, for this to be concluded, subjects need to be tested with novel stimuli (not presented during training) to see if what was previously learned "transfers" (Urcelay & Miller, 2010). Consider for example the concept of "same" versus "different". Objects in the real world do not have these attributes. A door cannot be described as same or different, unless a second door serves as a reference. Therefore, these terms refer to a judgment we make in comparing two objects or images, and their study in animals is thought to be a defining measure of cognitive ability and intelligence (see Wright, Kelly, & Katz, 2018, for a review). Are non-human species capable of learning such abstract concepts? A great deal of research has interrogated how pigeons, primates, and other animals learn the concepts same and different after extensive training (see Smirnova, Zorina, Obozova, & Wasserman, 2015, for an example with hooded crows; and Giurfa et al., 2001 in honey bees). In one approach to same/different learning (e.g., Wright & Katz, 2006), pigeons, rhesus monkeys, and capuchin monkeys were presented with two pictures. If the two pictures were the same, subjects had to touch or peck the lower picture to obtain food reinforcement. If the pictures were different, they had to touch or peck a reporting key to the side of the pictures to obtain reinforcement. Learning of the same/different concept was then evaluated by testing the animals with novel stimuli. Performance on the transfer trials improved with increases in the number of pictures used during training. Monkeys learned the same/different concept in fewer trials than pigeons. However, the fact that performance improved for all species with increases in the number of stimuli used suggests that the monkeys and pigeons used similar mechanisms.

Finally, further support in favour of the use of principles of learning in comparative cognition comes from the domain of tool use and construction in non-human animals (see Chapter 25, this volume). Indeed, numerous species have been observed to use tools in various ways and much of the research on non-human tool use has been conducted with chimpanzees and other primates (e.g., Price, Lambeth, Schapiro, & Whiten, 2009), but recent provocative evidence reports of extensive tool use and tool fabrication by several species of birds (e.g., Bayern et al., 2018). A notable example of tool use comes from studies with New Caledonian crows (*Corvus moneduloides*) by Alex Kacelnik and his colleagues. For example, in one experiment two wild-caught crows were given access to food placed in a transparent horizontal plastic tube with one end open. The food was arranged at various distances from the tube's opening, and twigs of various lengths were available for the birds to use to collect the food. The supplied twigs were readily adopted by the crows. Critically, on each trial, the birds selected twigs of the right length at a rate that far outpaced chance (Chappell and Kacelnik, 2002). In another study, food was placed in a miniature bucket and lowered into a clear plastic tube to test one of the wild-caught crows. To obtain food, the crow had to make a hook out of a piece of metal and use it to grab the bucket's handle, allowing the bucket to be pulled up and the food to be provided. Metal strips of various shapes were given to a wild-caught crow. Without much difficulty, the bird was able to modify each one in a unique way to serve as an effective hook (Weir and Kacelnik, 2006). Importantly, how the animals acquired the behaviour, that is, how they learn to make and use tools and what behavioural and cognitive processes are responsible for this type of behaviour, is considered a critical question in comparative cognition. An interpretation which is a topic of current discussions in this field is whether tool use and fabrication in the above-mentioned examples is a form of instrumental behaviour, reinforced by food that is obtained each time tools are used. Using Eurasian jays, carefully controlled experiments suggest that instrumental learning alone is insufficient to explain tool use (Cheke, Baird, & Clayton, 2011).

These and other examples of "complex" learning in non-human animals have led to heated discussions about "associative" and "cognitive" explanations. In that debate, associative learning is the "null hypothesis" upon which cognitive explanations are tested (Dickinson, 2012). If a phenomenon can be explained by current associative principles, then it must be associative. If the phenomenon lies outside of associative explanations, then it must be cognitive (see Jaakkola, 2014, 2015; Pepperberg, 2015 for a recent example). We argue that the fact that a phenomenon cannot be explained by associative principles should, rather than discarding the associative explanation, encourage students to develop better models to explain such complex phenomena. As can be observed by the examples mentioned above, this task shows that behaviourism (and associative learning) are a fruitful ground where such developments are likely to happen.

In summary, we have presented a brief historical review on behaviourism, and developed a few examples that suggest that animals are capable of dealing with representations of events previously experienced, and use these to guide future behaviour. Thus, we do not see the line distinguishing associative learning and cognition as being clearly defined by current discussions, because many phenomena previously touted as cognitive can now be accommodated by associative explanations. Similarly, we discussed how the notion of prediction error, which was developed under behaviourism, has illuminated research in diverse areas such as neuroscience, memory research, and social learning. The current discussion underscores the importance of studying behaviour and seeking explanations grounded in basic principles of learning, to gain a better understand of behavioural phenomena from a comparative perspective.

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3

ON STRENGTHS AND LIMITATIONS OF FIELD, SEMI-NATURAL CAPTIVE, AND LABORATORY STUDY SETTINGS

George W. Uetz, David L. Clark and Brent Stoffer

Introduction

Historically, ethology developed from the direct observations of animals in the field, characterizing behaviours in their natural environment (Beer 2020), while comparative psychology examined the "psychological ability" (e.g., learning and cognition) of animals in a lab setting (Dewsbury 2017). Both fields have morphed – perhaps merged – over the years, and the traditional placements of ethological studies in the field and comparative psychology studies in the lab are not quite as rigid. Comparative psychology has been positively influenced by fields like neurobiology and behavioural ecology, which encourage animal psychologists to think more about the organism's biological and evolutionary context. Likewise, ethology and behavioural ecology have begun to focus more on integrative and mechanistic approaches, with more rigorous experimental techniques and lab studies.

Our chapter seeks to examine the strengths, limitations, and considerations of methodological settings in comparative psychology experiments including field-based, semi-natural captive, and lab-based studies. While questions regarding whether field-based studies or lab-based studies are more appropriate will inherently depend upon the basis for the research question, there are broad considerations that investigators should make before, during, and after their study. After presenting some considerations, we then summarize our own research across a series of studies involving lab, field, and semi-natural mesocosms. We conclude by looking into the future and address how advances in technology and experimental approaches might improve the quality of all three approaches.

Lab or field?

Much has been made of the trade-offs in hypothesis testing by observing "natural" behaviour in the field vs. the "artificiality" of laboratory experimentation (Calisi & Bentley 2009). Observational studies in the field capture the behaviour of an animal *in situ* but can be challenging for several reasons. Field studies can require more time to accumulate sufficient data, making direct observation of subjects more difficult, and can lack control over potentially complicating variables. On the other hand, laboratory studies can be designed precisely to collect data that allows investigators to address detailed questions. They are, however, often criticized because they are conducted in an environment that by its artificial nature might influence behaviour. Between these two extremes may lie several other means of animal behaviour research circumstances that may offer alternatives that incorporate

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the best of both worlds. For example, research on animals in captive, yet natural, settings may be a compromise solution.

There are, therefore, a variety of considerations before conducting projects in any setting, some of which will be species-specific and some that might be broader concerns across taxa (see Table 3.1). An array of studies would be difficult or impossible to conduct in one setting or another. Thus, we emphasize that our goal is not to criticize field or laboratory settings, but rather, ensure that considerations in the experimental designs and interpretations of such studies are being made appropriately.

Table 3.1 A summary of questions experimenters might ask themselves before, during, or after the study when conducting field, semi-natural, or lab studies.

Experimental Design	*Timing*	*Consideration (Question?)*	*Example that Demonstrates the Problem or Provides a Solution*
Field study	Before the study	Is the full repertoire of behaviours mostly understood and described?	Multiple quantification methods to measure personality in the field (Tkaczynski et al. 2019)
		To what extent can the research question be tested in a field study where behaviours are often difficult to observe?	Acceleration sensors to detect animal movement otherwise difficult to observe (Brown et al. 2013)
	During the study	Can you identify individuals of your study organism in a field setting?	Tracking software to detect individual visual tags on animals in the field (Crall et al. 2015)
		Does the presence of a human observer impact the organisms' behaviours?	The use of radiotelemetry to quantify whether human observers have an effect on behaviour in capuchins (Crofoot et al. 2010)
	After the study	What was learned about the organism and its behaviours in a natural setting?	Testing field-experienced and lab-experienced male spiders in the field to ensure that male eavesdropping courtship was not a lab artefact (Clark et al. 2015a)
		Can the results be confirmed with more experimental control in a follow-up study?	Follow-up lab experiments revealed that male wolf spiders eavesdrop upon conspecific courtship by associating male courtship with female cues (Clark et al. 2012, Clark et al. 2015a; Stoffer et al. 2021)
Semi-natural captive	Before the study	What variables can be better controlled by providing a semi-natural setting?	The use of mesocosms to better understand the ecotoxicology of amphibians (Boone & James 2005)
		What is the appropriate amount of artificial manipulation to be done?	Associations with zoo visitors are positive for some species, but negative for others (Sherwen & Hemsworth 2019)

(*Continued*)

Table 3.1 (Continued)

Experimental Design	*Timing*	*Consideration (Question?)*	*Example that Demonstrates the Problem or Provides a Solution*
	During the study	Do the organisms appear to have an appropriately sized setting?	Large flight arenas for butterflies allow full interactions and an array of choices in mate preference studies (Westerman et al. 2019)
		Does the presence of semi-natural manipulations overly limit the broader implications of the results?	Semi-natural marine closure identified dolphin vocalizations, but the isolated population made it difficult to discern whether vocalizations were population-specific (Perelberg et al. 2010)
	After the study	Should standardized or species-specific rearing environments be utilized to compare within and across species?	Differences between dog puppies and wolf pups revealed despite standardized socialization and hand-raising by humans in an animal park (Gácsi et al. 2005)
Laboratory study	Before the study	How might the maintenance of the study organism(s) affect the outcome?	Cage size and enrichment influence jumping spider behaviours (Carducci & Jakob 2000)
		What is the influence of the social environment in which the study organisms are/were raised?	The perceived availability and phenotypes of potential mates during development affect subsequent mate preferences as adults (Stoffer & Uetz 2015, 2016a, b)
	During the study	What is the effect of feeding regime on the development and ultimate outcome of the experiment?	Feeding regime in a lab setting affects a secondary sexual character (Uetz et al. 2002), which affect mate preferences (Scheffer et al. 1996, McClintock & Uetz 1996)
		Are the results replicable across other laboratory contexts?	Given the evidence for learned eavesdropping, follow-up studies revealed that social facilitation occurs – male wolf spiders courted more in response to more conspecific males (Clark et al. 2015a)
	After the study	Can follow-up studies in the field or a semi-natural setting be conducted in order to assess the validity of the laboratory-based conclusions?	Given lab evidence that male wolf spiders court in response to conspecific male courtship, follow-up studies in the field confirmed such behaviours in field-experienced males (Clark et al. 2015a)
		Given the research question, what follow-up studies can be conducted to test hypothesis in closely related species?	Video playback in the lab revealed that experimentally manipulated ornamentation on the forelegs of wolf spiders increases receptivity from some, but not all, species studied (Hebets & Uetz 2000)

Considerations in field settings

Before the experiment

Field studies are foundational for many reasons but are perhaps ultimately best for particular research questions. In some cases, very little might be known about the animal in question, making field studies a necessary starting point. In other cases, studying the animal in a natural setting might be the only way to examine the behaviours and context(s) of interest. Further, knowledge about behaviour may be critical for conservation concerns, and studying these species in captive or lab settings is not appropriate. However, understanding higher-level research questions from a hypothesis testing perspective often presumes that we know a great deal about an organism's baseline behaviours, as well as the proper time and social context in which they occur. If baseline behaviours are already well-described, then the behaviour might well be studied in either a natural or laboratory setting, providing certain conditions are met. If such behaviours are not already well-described, then we argue that at least descriptive field observations are a necessary pre-requisite.

During the experiment

One concern with field studies may arise because the behaviours of interest might be simply too difficult to observe in the wild. In many cases, there might also be important, yet unknown impacts seen in field experiments because of uncontrolled environmental factors (Calisi & Bentley 2009). Researchers must ensure that the field study is being conducted at an appropriate time (seasonal and circadian rhythms), within an appropriate social context (territories), or in the correct habitat. It is also important to have insight regarding the organisms' complex natural habitat in which the studies are to be conducted. An additional concern is that it may or may not be possible to manipulate certain contexts or circumstances in the field in order to appropriately measure subsequent responses and test hypotheses. Ideally, such considerations would be addressed before the experiment itself. However, sometimes consequences of experimental design choice do not become apparent until such decisions are already made and data collection has begun.

After the experiment

We also encourage researchers to carefully reflect upon the implications of their study once completed. One must consider, for example, whether there was a sufficient sample size to extrapolate the field observations to a meaningful level of interpretation (i.e., are the results unique to the studied individuals, the entire population, or the species?). While assessing the replicability of a study is important regardless of where the study takes place (lab vs. field), it might perhaps be more important in a field study, due to the possibility of uncontrolled variables having unknown effects on the behavioural outcomes. For this reason, one must reflect upon the number of variables that often cannot be controlled in a field setting, and whether there are newly identified, measurable variables for which data should have been collected during the experiment. As a consequence of all these considerations, many field studies take more time to accumulate observations.

Considerations in semi-natural captive settings

Before the experiment

There are a variety of considerations before the study has been conducted that can improve the probability of obtaining meaningful results in a semi-natural setting. It should not be overlooked, for example, how imperative it is to utilize the literature and direct field observations to truly understand what types of environments the research is attempting to mimic. Perhaps the most difficult challenge in making such observations is that we have a tendency to observe the animals' environment from a human perspective, when in reality, the semi-natural setting needs to be replicable from the perspective of the study organism itself. We suggest, therefore, considering literature that focuses on the sensory biology of the study organism and the characteristics of the environment. Such an approach will better inform decisions related to which materials (color, size, shape) should be utilized, whether artificial materials can be substituted for natural materials, what size the semi-natural captive study should be, and whether enrichment needs to be included.

During the experiment

One must consider the appropriate semi-natural setting in which to conduct the behavioural studies. Maintenance of captive animals in outdoor pens, aviaries, and ponds ("mesocosms") allows observations of behaviour under conditions that might be seen in the wild (Gibbons et al. 1994). Animals in zoos and aquarium settings also provide opportunities for researchers to study behaviour of species that otherwise might be inaccessible, although confinement of the captive environment can sometimes lead to aberrant behaviours known as stereotypies (Kaufman et al. 2019). One possibility for future study in semi-natural zoo settings is the use of enrichment devices to measure cognitive abilities of many animals.

Smaller semi-natural captive settings ("microcosms") such as aquariums and terrariums, however, are more appropriate for smaller animals. Although microcosms have been used to study the impacts of environmental toxins (e.g., Boone & James 2005), they can also be used effectively in fine scale behaviour measures (Uetz et al. 2013). While the use of microcosms depends on organism size and scale, the smaller scale enables replication and manipulation of environment. For example, a number of studies with insects and spiders in lab microcosms constructed with materials from the natural habitat have yielded insights in a controlled setting that would not be possible in the field (Gordon & Uetz 2011).

Use of Radio Frequency Identification Devices (RFID) to track animal movements in semi-natural captive settings allows collection of continuous movements to assess the effects of environmental factors, temporal patterns, and interactions among individuals (Kalafut & Kinley 2020). Results could therefore be useful both to members of the zoo community interested in improving living conditions for captive animals, as well as researchers in animal behaviour and comparative psychology testing hypotheses of broader scopes.

After the experiment

When interpreting results from semi-natural captive studies, it might be tempting to view the results as if they were collected from the organism's natural environment. While semi-natural settings might bring together the benefits of both lab studies and field studies combined, they do not perfectly mimic the real world, making it important for researchers to frame their results appropriately and accurately. Results from semi-natural studies will yield many additional hypotheses that can be tested in the field, if that is the ultimate goal of the research question. For traditional ethologists perhaps more interested in implications of semi-natural studies in the real world, results from semi-natural studies can, therefore, provide pilot data for future field studies. For traditional comparative psychologists or others who conduct mostly lab studies, results from semi-natural studies instead can provide proof of concept that results in the lab seem to translate well into a field-like setting.

Considerations for laboratory study settings

Before the experiment

First, it is important to take into account what is already known about the organism, with respect to published qualitative and quantitative behavioural studies. The behaviours under analysis in the lab need to be assessed to ensure that such behaviours would be expected in a natural context. For example, in some cases, organisms that are reared in the lab do not behave to the same degree once assessed in the field (e.g., Meza-Hernández & Díaz-Fleischer 2006).

Second, researchers must consider the study organism's experience prior to being brought into the lab. Given the effects of mating status, age, diet, and social environment on behaviour, lab studies need to proceed with caution given that the experimenters often alter these parameters in a lab setting. Even in invertebrates, social experience prior to adulthood can affect subsequent mate preferences (see Stoffer & Uetz 2015, 2016a, b, 2017 and citations within). While many of these studies are conducted in the lab using audio and/or video playback techniques, it is not surprising that an individual's social environment affects subsequent behaviours given results from population-level analyses (e.g., Gwynne 1984).

Next, one must consider whether the study organism should be brought into the lab at all, given the organism's size, physical limitations, and the extent to which rearing conditions can be appropriately provided. While we are able to bring in thousands of wolf spiders on a yearly basis, such a scale of operations would be impossible for even modestly large study organisms. Finally, one must consider whether an overly simplified rearing environment in a lab setting might affect behavioural outcomes in unnatural ways. If the study organism were isolated during its rearing environment, then such a limited rearing environment might reduce its later social interactions.

During the experiment

Laboratory-based studies require experimental set-ups that are inherently different from natural contexts. Decisions regarding the physical location of the experimental trials (e.g., an arena, tank, petri dish, terrarium, aviary), the number of stimuli used for playback techniques (Dougherty & Shuker 2015),, the sensory *Umwelt* (Von Uexküll cit. in Brentari 2015) of the trial location (e.g., visual contrast, ambient noise), and other organisms used in the experiment, all should ideally be made prior to the experimental trials being conducted. However, one must look for behavioural indicators during the experiment itself that might suggest the organisms' responses are impacted by the experimental set-up.

Perhaps the greatest benefit of conducting a laboratory study is the ability to manipulate the study organism, a particularly useful strategy for physiological and genetic studies. Calisi & Bentley (2009) summarized a collection of noticeable differences in hormone levels, neural differences, variation in photoperiodic responses, and discrepancies in circadian rhythms in lab versus field studies. Many of these differences are likely to directly or indirectly affect additional behaviours. We therefore encourage researchers to compare field versus lab physiological measurements for their study organism, emphasizing that rearing in a lab environment can have unintended consequences on the underlying physiological and genetic expression levels.

After the study

We encourage researchers to reflect upon many of the aforementioned considerations after the study has been completed. We especially encourage follow-up studies in the field or a semi-natural setting be conducted in order to assess the validity of the laboratory-based conclusions. For example, male *Schizocosa ocreata* wolf spiders often court in response to video playback of conspecific male courtship, but no evidence of social facilitation was found (Roberts et al. 2006). Follow-up studies showed that field-experienced male *S. ocreata* courted in response to conspecific male courtship much more than lab-experienced males (Clark et al. 2012). These and further studies clearly demonstrated that in the field, male *S. ocreata* learn to associate courtship of other males with the presence of a nearby female (Clark et al. 2012, 2015a; Uetz et al. 2019; Stoffer et al. 2021). Perhaps most importantly, in an extension of lab findings to the field, a further study clearly demonstrated that such courtship eavesdropping does in fact occur (Clark et al. 2015a).

Careful approaches to research questions related to animal behaviour and comparative psychology are not likely to be entirely, or accurately, answered with only lab-based studies or only field-based studies. Certainly, such approaches require follow-up studies, further investigation, and careful framing of the results. Discovering differences between lab-based and field-based studies does not necessarily render such results to be useless. Instead, it speaks to the complexities of such behaviours and the importance of taking such differences into account when interpreting the results.

New approaches

Video playback – novel techniques with pros and cons

Studying the interaction between the behavioural components and sensory modes that comprise animal signals, and the way(s) in which they influence receiver decision making is an experimental challenge requiring novel approaches. Video and computer-based animation provides an effective means to manipulate stimulus appearance and behaviour in ways that are impossible to achieve with real animals. Since the discovery of video playback and digital manipulation in experimental studies of animal behaviour (Clark and Uetz 1990; Evans and Marler 1991; Macedonia & Rosenthal 1997), video animations have become valuable tools because they allow manipulation of morphology and/or behaviour while holding other factors (e.g. size or courtship effort) constant, and eliminate interaction between focal and stimulus individuals, which can bias experimental outcomes. Digital playback has been used in studies of many animal taxa (see reviews in Woo & Rieuchau 2011; Chouinard-Thuly et al. 2017).

Techniques for constructing video playback stimuli generally fall into three categories (Rosenthal 2000).

1. <u>*Recording and playback with live animals in the field*</u> was used by Burford et al. (2000) to determine responses of male and female *Uca tangeri* fiddler crabs to claw waving behaviour. Pope (2000) examined the claw waving display of *Uca pugilatoris* fiddler crabs by presenting video obtained from captive crabs in semi-natural pens.
2. Video playback stimuli can also be prepared from *frame-manipulated digital video* (see Figure 3.2) with image and animation software (see Uetz & Clark 2014), although it is important to create multiple representative stimuli (i.e., exemplars) to avoid pseudoreplication (McGregor 2000).

Figure 3.1 Male *Schizocosa ocreata* with two digital video stimuli on iPod® screens.

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3. Digital animation of "wireframe" animals (Rosenthal 2000) uses a digitized image of the animal that is applied as a "skin" over the wireframe, and the entire sequence of behaviours is created *de novo*. This has real advantages in that the investigator has complete control over the unique exemplar (avoiding pseudoreplication), so long as the behaviours of the stimulus animal elicit an appropriate response.

Video playback studies have been criticized for various reasons, including a mismatch between video screens and animal visual acuity, critical flicker fusion frequency and color perception (see reviews in Woo and Rieucau 2011; Chouinard-Thuly et al. 2017 and references within). It is critically important that all video playback research programs first demonstrate that focal animals perceive video images and interpret them as real. Our earlier studies demonstrated that the visual acuity, low critical flicker fusion frequency, and spectral range of jumping spiders, wolf spiders, and some of their vertebrate predators allow them to perceive video images, interpret video images as real, and behave appropriately to such video images (Clark & Uetz 1990; Uetz & Clark 2014; Uetz et al. 2016; Rubi et al. 2019). Once our approach was validated, use of synthetic digital playback stimuli allowed us to conduct a series of experimental studies using digital playback of video and vibratory/seismic signals to examine mate preferences in female *Schizocosa ocreata* wolf spiders (summarized in Uetz & Clark 2014; Uetz et al. 2016).

Studies of mate preference in many species suggest that females show ordered preferences for size or expression of male traits, both within a single sensory mode, or in covarying modalities – although some studies suggest comparative evaluation of mates rather than absolute preference hierarchies (Bateson & Healy 2005; Uetz et al. 2017). Recent studies have successfully combined video playback with audio playback of seismic vibration using substrate-mounted speakers and piezoelectric devices (Uetz & Roberts 2002; Roberts et al. 2007; Uetz et al. 2016; Kozak and Uetz 2019; Stoffer and Uetz 2017; Uetz et al. 2017) (see Figure 3.3). These techniques allow us to experimentally manipulate multiple signal components and/or the use of multimodal signals for both intended and unintended receivers. In studies with isolated individual sensory modes and multimodal (combined) signals, female wolf spiders showed ordered preferences for tuft size and vibration amplitude. A comparison of no-choice and two-choice tests revealed that females exhibited transitive preferences, consistently

Figure 3.2 Still shot of digital courting male *S. ocreata* stimulus on iPod® screen.

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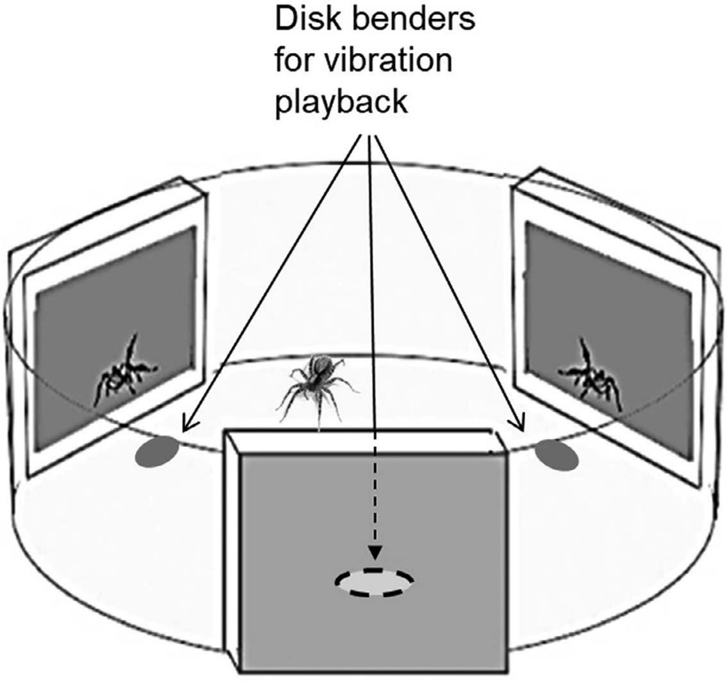

Figure 3.3 Diagram of multimodal playback mate choice arena, with two iPods and piezoelectric disk benders. © G.W. Uetz, used with permission.

choosing males with larger tuft size or higher amplitude vibration (Uetz and Norton 2007; Uetz et al. 2017). However, the combination of video and vibration playback also allowed for experimental 'cue-conflict' (negative trait covariance) choice tests. Choice tests with multimodal playback showed that females made predicted choices when male traits covaried positively, but when information in cues conflicted, females showed a bias for visual signal trait expression (tuft size) over vibratory signals (Uetz et al. 2017). These studies demonstrate that differences in behavioural responses to manipulation of cues from digital video and vibration playback can provide valuable insights about recognition and interpretation of complex signals and their components.

Computer animation and digital manipulation have also allowed us to explore alternative evolutionary trajectories to investigate extreme male dimorphism in the dimorphic jumping spider, *Maevia inclemens*, where the two male morphs are so distinctive that they resemble entirely different species (Clark & Uetz 1992, 1993; Clark 1994). Based on their characteristics, we created a "hypothetical ancestral male" that might reasonably have existed prior to morph divergence, as well as "digital chimeras" with switched morphologies to test hypotheses about whether morphology or behaviour was more important in species recognition. As it turns out, females responded more often to behavioural displays, regardless of superimposed morphologies (Clark and Uetz 1993).

Robotic animal stimuli in field and lab

While video playback has advantages over other methods of stimulus presentation, it is largely limited by the nature of two-dimensional visual images. To a degree, virtual reality can address this problem (Peckmezian & Taylor 2015), but depending on the test subject and perspective, the stimulus may still lack the real-life feel of an actual animal model. Historically, the study of fish and birds using dead animals or three-dimensional models produced of wax or wood (Rowland 1999), may have contained a sense of realism that video may lack. However, a human-operated model may be compromised by the variation inherent in multiple presentations and the nuances associated with the interpretation of the behaviour pattern by the experimenter. The use of 3-D scanners and printers has made the process of producing models of animals easier, and other advances in technology (e.g., miniaturization of electronics; easier data transmission) make controlling and reproducing accurate behaviour patterns robotic animals in a variety of species (Patricelli et al. 2006; Klein et al. 2012; Woo & Rieucau 2011).

Because of their highly stereotyped display behaviour, one of the most well-studied groups of animals where robots have been used to study behaviour has been lizards (see references above). Robotic models allow test stimuli to be presented in the field where resident lizards have well-established territories and are likely to display naturally to a potential intruder. Several studies conducted by co-author Clark and colleagues have used robotic models (Clark et al. 2015b, 2016b; Dufour et al. 2020). Life-like robotic models were constructed of a wooden dowel internal skeleton, and "skins" for the bodies were constructed using high-resolution photographs of live adult lizards from an onside perspective. In field studies, we sought out resident lizards with established territories and presented them with a robotic model (see Figure 3.4). By presenting the test stimulus robotic lizard model to test subjects in their natural habitat and within their own territories, we believe that we obtained natural responses by test subjects.

Combination approaches

Video playback can be utilized in conjunction with other behavioural approaches in meaningful ways. For example, Rubi et al. (2019) examined how courtship and body coloration affect the conspicuousness of male wolf spiders (*Schizocosa ocreata*) to avian predators. Captive blue jays (*Cyanocitta cristata*) were presented with virtual male spiders in an operant experiment to determine spider detectability (Rubi et al. 2019). The results suggest that male *S. ocreata* can be both

Figure 3.4 A robotic lizard in the field with a live Galapagos lava lizard (*Microlophus* sp.) responding.
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conspicuous *and* cryptic to avian predators (depending on movement) and demonstrate the benefits of using digital playback to address questions about the evolution of behavioural and morphological traits.

A more recent development by some of our associates is virtual reality (e.g., Peckmezian & Taylor 2015), which offers the possibility of three-dimensional image playback to study, for example, behaviour, effects of habitat lighting and visual background motion on signal visibility and discriminability, constraints imposed on signals by the habitats in which they are displayed. Video playback can also be used in conjunction with neurophysiological recording. Recently, Winsor et al. (2021) combined video playback with eye-tracking technology and software to examine gaze direction in a jumping spider.

Conclusion

Questions regarding whether field-based studies or lab-based studies or semi-natural contexts are more appropriate will inherently depend upon the basis for the research question. We encourage researchers to consider whether their research questions are guided by the focal organism or a broader hypothesis. Based on the considerations presented, we also suggest that there are particular organisms and research questions that might be better suited to a field environment or lab environment (e.g., Krogh's principle – Lindstedt 2014).

We also encourage researchers to consider whether they are more interested in proximate explanations, ultimate explanations, or both. Because proximate questions are more likely to be developmental, genetic, hormonal, or physiological, the ability to have more experimental control in a lab-based setting is invaluable. Some comparative approaches using physiological techniques suggest, for example, focusing on studying organisms that have rather unusual adaptations or traits that are uniquely well-suited. Such an approach makes intuitive sense, but the question remains as to whether such physiological changes are best measured naturally within the organisms' extreme or unique environments. Given that research questions based on ultimate explanations focus greatly on the comparative nature of comparative psychology, it might seem reasonable to examine behaviours on a level playing field within a lab setting.

Finally, we urge researchers to consider how naturalistic a lab-based setting is for their particular species or group of species that is being compared. While there may be no final answer as to whether field studies or lab studies are more appropriate, we hope to have at least convinced readers of how important it is to consider the pros, cons, and considerations for their particular study organism and research question. We suggest that ultimately, a blend of studies is ideal, i.e., either a mixture of field-based *and* lab-based studies or the use of semi-natural captive studies or mesocosms. Perhaps it is for that very reason that as the fields of ethology and comparative psychology have progressed and morphed over time, ethology has informed comparatively psychology, and comparative psychology has informed ethology.

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4

ONTOGENY OF BEHAVIOUR

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If the end of life is usually easy to identify, it may be tricky to determine exactly when the life of an organism begins. In this chapter, we will focus on multicellular organisms. We may define the beginning of life as the first cell division of the initial single cell which will give rise to the organism. There are several modes of reproduction, which can be asexual or sexual. Sexual reproduction involves germinal cells and includes different forms such as hermaphroditism (an individual possesses both ovarian and testicular tissues) and gonochorism (sperm and egg production in separate individuals). Asexual reproduction includes parthenogenesis, in which an individual develops from an unfertilized egg. The life cycle of an animal is a sequence of different stages that can occur in aquatic and/or terrestrial milieux. For example, in frogs and toads, fertilized eggs are released in water and, following hatching, tadpoles will go through several stages of transformations before developing lungs and being able to adopt a terrestrial lifestyle. Early development of many vertebrates, including humans, also starts in a liquid milieu before birth. The case of insects with metamorphosis is intriguing. We can consider that insects are born twice: the first time when the egg hatches into a larva, and the second time when the larva becomes an adult (imago). In many insects, the larval life can be much longer than the imago life. Some cicadas, such as *Magicicada septendecim*, show an impressive life cycle including the longest synchronized developmental phase in nature. Adults are active only for about a month. Females lay eggs in trees and after hatching the nymphs burrow and remain underground for 17 years, during which they feed on roots and xylem fluids and go through several juvenile stages. Then, groups of young cicadas emerge together to reproduce. Other insect species are characterized by a short life cycle, such as *Drosophila* (total cycle completed in 10–18 days, depending on the temperature), with only few days at the larval stage. At the other extreme, some vertebrate species can live up to more than two centuries such as tortoises, whales or sharks.

Even if life is not only about finding food, a shelter, a sexual partner and to avoid predators, since the beginning of life to death, animals will have to deal with these problems. It appears that they have been prepared over evolutionary time to behave adaptively at different life stages. The study of ontogeny is the study of these adaptations. It addresses a so-called *proximate* level of analysis, one of the 'how' questions in Tinbergen's famous conceptual framework (Tinbergen 1963; see also Burghardt and Drickamer, Chapter 1, this volume): *How did a trait develop?* Ontogeny of behaviour refers to the processes underlying the development of behavioural traits during the entire life of an organism. We will now explore some of these processes.

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MATURATION AND EXPERIENCE

Maturation and experience are two interconnected and important aspects of behavioural ontogeny. Maturation is the process of proliferation and differentiation of cells, tissues and organs during development. Experience refers to the effects of both external and internal environment including the stimulations experienced during sensorimotor integration. Experience can have inducing and both facilitating and inhibiting effects on maturation. In social insects, for instance, the rearing environment, particularly nutrition, determines whether a larva will mature into a large and long-lived reproductive individual with well-developed ovaries (queen, facilitating effects on maturation) or into a smaller individual (worker, inhibiting effects on maturation) with undeveloped ovaries and a short life span (Wilson 1971). The behavioural repertoire of queens and workers and their role in the colony is extremely different. In most social insects, becoming queen or worker is not based on heritable genetic differences but on chemical modifications of DNA, such as methylation, that do not change the DNA sequence (Weiner and Toth 2012), i.e. epigenetic modifications (see text box). In oscine songbirds such as male zebra finches (*Taeniopygia guttata*) that learn to sing from an adult tutor during a sensitive period, exposure to the song model enhances maturation of neural networks (Wilbrecht et al. 2002).

EPIGENETICS

Epigenetics is the study of molecular mechanisms regulating gene expression without modifying their DNA sequence. We know that the cells that compose the same organism have all the same genetic information but retain their unique identity: for example, a neuron is phenotypically and functionally different from a muscular cell. During the processes of cell division (mitosis and meiosis), modifications such as DNA methylation can block or favor the expression of genetic information. In the history of behavioural research, the term "epigenetics" also refer to an approach emerging as a critical appraisal of the concept of instinct or innate behaviours. Kuo (1967) defined behavioural epigenesis "*as a continuous developmental process from fertilization through birth to death, involving proliferation, diversification, and modification of behaviour patterns both in space and in time, as a result of the continuous dynamic exchange of energy between the developing organism and its environment, endogenous and exogenous. The ontogenesis of behavior is a continuous stream of activities whose patterns vary or are modified in response to changes in the effective stimulation by the environment*". Not surprisingly, this definition is very similar to our definition of ontogeny given above.

Epigenetics has opened up very promising avenues of research in various fields, including animal behaviour. In a beehive, the larvae of workers and queens are genetically identical, but depending on the diet and care given, a larva will become queen (breeder, with ovaries) or a worker (see above). Recent work has shown that when the expression of the enzyme responsible for DNA methylation is altered in larvae fed to become workers, they develop ovaries shaped like those of queens. This indicates that the royal jelly contains substances that inhibit DNA methylation (Chittka and Chittka 2010). Exposure of adults (males and females), pregnant females (mammals) or eggs (birds) to environmental stress such as chronic exposure to noise or frequent cage exchanges can have both trans- and inter-generational effects (Guerrero-Bosagna et al. 2018). Moreover, the offspring of (control) female mice injected with the sperm of stressed males exhibit significant behavioural differences with offspring from control groups for different well-established tests to measure stress and anxiety in rodents (Gapp et al. 2014). These results demonstrate that a chronic exposure to stress can have effects both on the soma and the germ lines and highlight the importance of considering epigenetic effects on the expression of behaviour.

The earlier stages of embryonic development include a rapid proliferation and differentiation of cells, orchestrated by architectural genes called homeotic genes. Hox genes are very unique homeotic genes that organize the succession of body parts from front to back in arthropods and vertebrates. Beyond homeosis, organogenesis and morphogenesis, some Hox genes also control behaviours such as stereotypical motor patterns that are the primary means by which animals interact with their environment. For example, expression of Hox gene Deformed (Dfd) is critical for feeding motor patterns in *Drosophila* (Friedrich et al. 2016). This maturational organization during embryonic life is shaped by experience with both external and internal stimulations. For example, in birds, asymmetrical stimulation of the right eye due to the position of the embryo in the egg (which causes the left eye to be occluded because it is oriented towards the body) has profound effects on different aspects of behavioural lateralization after hatching such as food pecking behaviour or locomotion (Chiandetti and Vallortigara 2019). Experiments with several animal species have shown that having a lateralized brain can enhance the capacity to perform two tasks simultaneously. For example, strongly lateralized (light exposed) were better than weakly lateralized (dark incubated) chicks (*Gallus gallus domesticus*) in executing dual-tasks at the same time: finding food and being vigilant for predators. This finding suggests that cerebral lateralization enhances brain efficiency in cognitive tasks that demand the simultaneous but different use of both hemispheres (Rogers et al. 2004). In the late stages of development, embryos are sensitive to different signals provided by their social environment, mainly their mother. For example, prenatal acquisition of individual auditory recognition of the parent has been demonstrated in several species of birds (see Rossi and Derégnaucourt 2020 for a review). In the superb fairy-wren (*Malurus cyaneus*), a species that undergoes brood parasitism by a cuckoo species, the Horsfield's Bronze-Cuckoo (*Chalcites basalis*), females call to their eggs during the late stage of development and, upon hatching, nestlings produce begging calls with key elements from their mother's incubation call. This strategy may allow both parents to detect foreign cuckoo nestlings (Colombelli-Negrel et al. 2012). In the Zebra Finch (*Taeniopygia guttata*), the parents acoustically signal high ambient temperatures (above 26°C) to the embryos by producing a particular call. Exposure of embryos to these acoustic cues alone adaptively alters subsequent nestling begging and growth in response to nest temperature and appears to influences individuals' reproductive success and thermal preferences as adults (Mariette and Buchanan 2016).

Following birth, young animals are classified either as precocial or as altricial, involving different developmental programs. Precocial animals are usually mobile and can feed by themselves except in mammals where they need the maternal milk for several weeks after birth. Precocial birds also need their parents, especially their mother as a warm source for thermoregulation. In altricial animals, which include humans, the young are extremely dependent on their parents for protection, thermoregulation, and food, and they are usually not able to leave the nest before a couple of weeks at least. A human baby will start to crawl between 6 to 10 months and to walk around 12 months. In the first minutes of aerial life, a young bird starts begging or a young mammal is able to find the maternal nipples. The begging response of gull chicks to the red spot on the parental bill is one of the well-studied cases of behavioural ontogeny in ethology (see ten Cate 2009 for a review of Tinbergen's work). In altricial animals, it may take several days before the eyes open and it is likely that chemical compounds, together with sounds emitted by siblings and parents, will help the young animal to discover its environment. For example, in the European rabbit (*Oryctogalus cuniculus*), a mammary pheromone has several functions such as localizing the nipples and promoting appetitive learning of novel odorants. Such learning could have long term effects when the young animals become autonomous in their food and mate choices (Coureaud et al. 2010).

In several species, young animals exhibit adaptive responses to predation risks at earlier stages of development. In great tits (*Parus major*), differential use of parental alarm calls elicits different adaptive predator-avoidance behaviours in nestlings. Great tit parents produce acoustically distinctive alarm calls for the two main nest predators: the Jungle Crow (*Corvus macrorhynchos*) and the Japanese Rat Snake (*Elaphe climacophora*). Nestlings crouch down inside their nest cavity in response to alarm calls given for a crow, while they flee the cavity in response to alarm calls given for a snake. The two responses help nestlings to selectively evade those predators, because crows snatch nestlings from the nest entrance, whereas snakes invade the nest cavity (Suzuki 2011). Depending on the life history traits of the considered species, different developmental programs will emerge. Such programs could open sensitive periods to external stimuli that induce long lasting effects. This example highlights that some innate programs prepare the animals since birth to a changing environment.

The interaction between an endogenous program and the effects of the environment is also well illustrated by studies of migratory behaviour in birds. In migratory birds, endogenous daily (circadian) and annual (circannual) rhythms serve as biological clocks that provide the major basis for their temporal organization (Gwinner 1996). Normally day active birds become nocturnal while migrating. This switch in circadian rhythmicity twice a year during ontogeny is accompanied by many neurophysiological changes such as enhanced night vision and sensorimotor integration of vision-mediated magnetic and/or star compass information for night-time navigation (Mouritsen et al. 2005). It has been proposed that, in first-year migrants, the time program for autumn migration plays a major role in determining migratory distance, thus providing the vector component in a mechanism of vector navigation (Wiltschko and Wiltschko 2015). In late winter and spring, individuals will often return to the area where they were born. Both migratory tendency and navigation appear to be under a strong genetic determinism. Indeed, in captive birds tested in Emlen funnels (a special type of cage used to measure the migratory behaviour of birds), both the amount of migratory restlessness and the directions have strong genetic bases. In crossbreeding experiments, birds of the same species belonging to populations with different migration patterns had offspring with intermediate behaviour, thus indicating that migratory restlessness as well as directional preferences are inherited from the parent birds in an intermediate model (Berthold and Querner 1981). Migratory activity exhibits inter-individual variability in partial migrant species (some individuals do migrate whether others migrate less far or stay on the breeding grounds during winter) and can also be drastically modified by several factors (Delmore et al. 2020). For example, since the 1950s, blackcaps (*Sylvia atricapilla*) began to winter in Great Britain while some of their counterparts continue to migrate to the traditional wintering grounds in Africa. Several findings across taxa support that partial migration is not based exclusively on genetic factors but is also driven by environmental conditions (Hegemann et al. 2015).

A milestone in ontogeny is reaching sexual maturity. Depending on the species, this can occur relatively fast in the first weeks of life, or after a long period of several years of development as in humans. In some species, only a fraction of individuals reaches sexual maturity. Such processes are under the control of hormones or pheromones. Developmental and seasonal changes in hormonal levels, especially testosterone, can induce reproductive behaviour. For example, in many songbird species, testosterone induces singing activity in spring. The hormonal milieu is important also in the early stages of development during both pre- and perinatal life. Testes removal in a newborn rat induces the lordosis response in the neutered adult male. Although genetically male, the castrated male behaves like a female. Conversely, impregnation of the brain with male hormones produced both during embryonic life and perinatal development prevents the female behaviour of lordosis and induces the characteristic mounting behaviour of the male when the female becomes adult (MacLusky and Naftolin 1981). In many species, sexual maturation is accompanied with changes in personality (Cabrera et al. 2021). In studies of non-human animals, personality is defined as physiological and behavioural differences among individuals of the same species, which are stable over time and across different contexts or situations (Carere and Maestripieri 2013; see also Dingemanse and Réale, Chapter 23, this volume). Such changes after sexual maturation have been described in humans (Caspi et al. 2005) and a number of other animal species across taxa such as the domestic cow, which shows inconsistent behavioural response to novelty before and after puberty (Neave et al. 2020). However, species such as the rat (Ray and Hansen 2005) show more stable personality traits (e.g. boldness, exploration or activity) from juvenile to adult stages. These interspecific differences in stability of personality across ontogeny may be related to changes in internal factors such as hormone profile, but also to changes in physical or social environments.

As we have already mentioned, temporal patterns of activity can change during ontogeny such as in migratory species. Other changes can occur with senescence. For instance, in octopuses (*Octopus vulgaris* and other species), both males and females go through a senescent stage before death: the males after mating, the females while brooding eggs and after the eggs hatch. Senescent males stop eating and show undirected movements, females stop eating already while brooding since they guard the eggs from predators. They will not resume eating after the eggs hatch and will not shelter (Anderson et al. 2002). Social insects modify their behaviour throughout their life and perform the most dangerous tasks at the end of their life. The lifespan of a honeybee worker (*Apis mellifera*) is about 40 days. Depending on its age, a honeybee will have different roles: first as a nurse, then as a nest keeper and finally as a forager or guard, the risky tasks (Robinson 1992). Social insects show many features that are different from those of other animals, including most social vertebrates. The hallmark of insect societies is their efficient colonial organization, based on reproductive division of labor, the specialization of individuals in a given task. Only few individuals reproduce (queens) while most of the society members forego direct reproduction and instead work for the colony (workers). Workers perform several diverse tasks, from caring for their mother's brood to nest maintenance, foraging and colony defense (e.g., Wilson 1971). Workers show temporal polyethism: a mechanism of division of labor, a method of task allocation, which is basically ubiquitous in social insects. The type of task an individual performs is correlated with its age, as in the example of the honeybee above. Young workers take up in-nest activities (e.g. brood and queen care, nest maintenance) while old workers work mostly as foragers, patrollers and guards at the nest entrance. In principle, this mechanism can be very simple. In some species, task specialization is ensured by individuals of different morphological castes. In general, queens are typically larger than workers, and workers can have different size and body shape (Figure 4.1).

Different models exist to explain division of labor and its relation to colony organization (Beshers and Fewell 2001). The most well-known is the response threshold model, which posits that individuals differ in their sensitivity, and therefore in their responsiveness, to biologically relevant stimuli present in the environment and associated with specific tasks. This difference in sensitivity alone can produce the emergence of division of labor (Robinson 1992; Bonabeau et al. 1996). For instance,

Figure 4.1 An extreme example of caste polymorphism is ants. In this species of African driver ant, *Dorylus molestus*, the queen is much larger than the workers. However, they share the same genetic information and the different morphology, physiology and behaviour are the result of different developmental conditions.

Image by Daniel Kronauer, reproduced from Kronauer (2020) with permission.

in honeybees, individual differences in sucrose responsiveness correlate with individual tendencies to forage either for pollen or nectar (Pankiw et al. 2001). Similarly, in ants, workers differ in their responsiveness to sucrose, and in their learning success in olfactory conditioning experiments. Olfactory learning abilities are usually better in foragers than in nurses, in agreement with their higher sucrose responsiveness (Perez et al. 2013). Therefore, responsiveness to stimuli and cognitive abilities change across the life of a social insect worker.

The response threshold model gives us a straightforward mechanism to interpret and explain the ontogeny of division of labor. Nevertheless, the reality is more complex. There are two factors that must be considered: intra-individual variability, the actual consistency of individual behaviours, and inter-individual variability, described for instance as personality. In a colony, the presence of workers with a high intra-individual variability may allow rapid adjustment to external fluctuations. Conversely, reduced within-individual variability may result in a more efficient specialization in task performance, and therefore reduce the costs of task switching (Jeanson 2019). It is challenging to understand the factors influencing the ideal balance between flexibility and canalization, which likely vary with the developmental stage of the colony and some key external factors, such as availability of resources and presence of competitors and parasites.

It is well acknowledged that social insects, such as ants, show different personality at the individual and colony level in several behaviours. There is an association between personality traits and cognitive traits, which affects task allocation. For instance, in individual carpenter ants, *Camponotus aethiops*, consistent individual differences in exploratory activity are related to learning performance and to cognitive judgement bias, the propensity to anticipate either positive or negative consequences in response to ambiguous information (d'Ettorre et al. 2017; Udino et al. 2017), which may influence foraging strategies. Personality predicts the probability to perform tool use in ants, with more proactive individuals having a higher probability to become tool users when previous tool users were removed from the group (Maák et al. 2020). This suggests that, instead of extreme task specialization based solely on temporal polyethism, variation in personality traits within the colony may influence division of labor. Therefore, the ontogeny of behaviour in social insects is the result of an interplay among several factors, among which it is important to consider both behavioural plasticity (intra-individual variability) and personality (inter-individual variability).

Death is the final stage of ontogeny. In some ants and bees, workers have been observed to leave the nest before dying. Being alone and isolated while dying might be a way to avoid spreading diseases to the colony (Heinze and Walter 2010; Rueppel et al. 2010).

GENES AND EXPERIENCE

The debate about "Nature vs. Nurture" has been a long lasting one. During the last century, there was a persistent debate between mainly American psychologists advocating for the prevalence of experience on the psychobiological basis of behaviour (behaviourism) and European biologists defending the so-called innate mechanisms (ethology). If there is still a strong interest nowadays for issues linked to the distinction between nature/nurture and culture, it is currently established that ontogeny is an interactive process between genes and environment in the development of behaviours (Hinde 1970) and that neither genes nor environment have a prevailing effect. Three paradigms were intensively used in behavioural research to disentangle the genetic effects from environmental effects and experience: (1) to raise an animal in social isolation from conspecifics before exposure to controlled stimuli; (2) cross fostering experiments in which young are raised by adults that are not their biological parents; (3) cross breeding experiments in order to produce inter-strain and inter-specific hybrids (Derégnaucourt 2010).

For a long time, it was established that a behaviour would be considered as innate if it would appear in animals raised in isolation from others. But such isolation experiments were criticized since an individual isolated "from fellow-members of his species is not necessarily isolated from the effect of processes and events which contribute to the development of any particular behaviour pattern" (Lehrman 1953). Such experiments also raise ethical issues. For example, using methods of isolation and maternal deprivation, the studies conducted by Harlow and his collaborators (1958; 1965) highlighted the importance of filial attachment and especially tactile contacts on primate development. Such studies would not be authorized nowadays by any ethical committee since the results were dramatic: young monkeys showed disturbed behaviour even after being reintroduced in a group.

Experience includes learning, which is defined as the effect of experience on behaviour. Selection should favor investment in neurophysiological mechanisms underlying learning when there is environmental variability. Learning is social when it occurs through the observation and/or interaction with other individuals. Imprinting is considered a form of social learning of a "model" that occurs at a particular life stage, typically early in life. It is characterized by a sensitive period in which experience has a strong effect on future behaviour and by the life-long persistence of the learning. Imprinting is critical in the development of recognition and social attachment, as described in the historical experiments with graylag goose performed by Konrad Lorenz in the 1930s. Social attachments made early in life may also influence behaviour later in life (sexual imprinting), such as mate choice, in many animals (Bateson 1966) including humans (Bereczkei et al. 2004). Imprinting is not exclusive to vertebrate species. Wood ant workers (*Formica polyctena*) must handle brood of their own species during the first weeks of adult life to be able to take care of them instead of treating them as food (Jaisson 1975). Non-social early experience with plant odors can also induce an environmental preference in ants (Jaisson 1980), a process similar to habitat imprinting, as observed for example in the Pacific salmon (*Oncorhynchus* spp; Putman et al. 2013).

Imprinting can happen before birth. Prenatal olfactory learning has been demonstrated in many animals and affects development and behaviour. In mammals, prenatal learning of chemosensory stimuli may determine food preferences after birth as flavors of the mother's diet pass rapidly into the amniotic fluid and reach the fetus. Rabbits exposed as fetuses to the odor of cumin are selectively attracted as neonates to this odor (Coureaud et al. 2002). Recognition of nestmates in ants may be influenced by experience at the larval stage, before metamorphosis. In the ant *Aphaenogaster senilis*, exposure to chemical cues of a different colony during pre-imaginal life affects recognition abilities of adult ants, particularly if the familiarization process occurs during the first larval stages (Signorotti et al. 2014), suggesting a sensitive period for this form of pre-natal imprinting and a complex picture in the development of nestmate recognition in general. Recognition of group members is of paramount importance in social insects, which rely on efficient discrimination between friend and foes based on learning of idiosyncratic chemical cues such as cuticular hydrocarbons (colony odor, see d'Ettorre and Lenoir 2010 for a review).

Besides imprinting, social learning often involves foraging behaviour. Feeding, including prey capture and food preferences, can change under parental influences and experience. For example, in felids, techniques of prey capture and killing improve with the experience of live preys, often provided by the parents. Social learning allows transmission of food preferences in rats (*Rattus norvegicus*) by interaction with demonstrator individuals (stimulus enhancement, Galef and Wigmore 1983) or transmission of feeding techniques, as in bumble bees (*Bombus terrestris*), which learn to become nectar robbers when they find flowers with holes at the base made by conspecifics to take nectar without effort (Leadbeater and Chittka 2008). Imitation allows foraging traditions to be transmitted from one generation to the next, as in banded mongooses (*Mungos mungo*), in which juveniles copy the foraging technique they observed as pups and continue to prefer this technique as adults (Müller and Cant 2010). Complex forms of social learning, such as teaching, may be involved in the ontogeny of foraging behaviour. Meerkats (*Suricata suricatta*) are cooperative breeders living in South Africa. The young are mostly produced by a dominant couple but are reared by all members of the group. When the pups are about one month old, they start following foraging groups, begging for preys. Adult helpers modify their foraging behaviour in the presence of pups. They stay close to the pups when they bring them a prey and they stay longer with younger pups. If the prey escapes, the adults bring it again to the pups (Thornton and McAuliffe 2006). This is considered as an example of true teaching because it fits three requirements: (1) the modification of the behaviour of the teacher in presence of naïve individuals to facilitate learning; (2) the teacher incurs some immediate costs (e.g. slower foraging time/efficiency, energy spent to monitor the pupil); (3) the pupil learns something faster than without teaching (Caro and Hauser 1992). Following this definition, individual ants can also teach the location of a food source to a naïve nestmate by tandem running (Franks and Richardson 2006).

Social interactions are important also when they do not appear to have a specific meaning. Play is a still underestimated component of psychobiological development of non-human animals (see Palagi and Pellis, Chapter 16, this volume). Play is common in young animals of many species but there is accumulating evidence of play behaviour in adult animals (Burghardt 2005). Behavioural expressions of play are evident in pets even while adults, and could be a consequence of domestication. Neoteny is defined as the retention of conspicuously juvenile characteristics into adulthood, and has been proposed as an important mechanism in human evolution by favoring learning and creativity. Neoteny is also an important component of the self-domestication hypothesis during human evolution (Lorenz 1950; Sánchez-Villagra and van Schaik 2019).

THE ROLES OF GENES AND ENVIRONMENT: THE CASE OF BIRDSONG LEARNING

If language is unique to humans, vocal learning – an important component of language – is present in a few taxonomic groups of animals including Oscine songbirds, about half of the existing bird species. Oscine songbirds learn to sing by imitating conspecifics, mainly adults. Species have been traditionally classified in two groups regarding their abilities for vocal learning even if this dichotomy sounds too simplistic nowadays (Martins and Boeckx 2020): age limited learners and open ended learners. In age limited learners, young birds learn to sing during a sensitive period early in life. During a sensory phase, the young bird memorizes a song model, usually the father's song (Figure 4.2). During a subsequent sensorimotor phase, the bird will compare his own song with the memorized model.

In the Zebra Finch, considered as the flying mouse of birdsong research, young males learn to sing during a sensitive period spanning from 25dph (day post hatch) to 90dph when song "crystallizes" and will not change for the rest of life. In this species, the sensory and the sensorimotor phase overlap, while in the white crowned sparrow these two phases are separated by several weeks. In open ended learners, such as the Nightingale, new learning can occur every year with opening and closing of new sensitive periods for learning. During ontogeny, singing starts with a subsong, the avian equivalent of human babbling, before the first signs of learning occur in the so-called plastic song, which lead then to a final crystallized song. If some species show mimicry to sounds produced by other species, such as the European starling, others stick to conspecific sounds or at least show a clear preference for conspecific songs when given the choice between conspecific and heterospecific models during the sensory phase. Young birds of some oscine species are able to learn heterospecific models or synthetic models very different from the conspecific songs when juvenile, but these sounds disappear in crystallized songs when adults. Such a selective attrition of sounds in the song occurs as a natural process for many species of oscine songbirds. For example, wild young male field sparrows, *Spizella pusilla*, and white-crowned sparrows, *Zonotrichia leucophrys*, often sing several song types when first establishing territories. Then, they select one, usually the song that best matches a neighboring rival's songs at the site where the young male is establishing his first territory, which is often remote from the birthplace (Nelson and Marler 1994). Such imitation could facilitate mutual benefits through a decrease of agonistic interactions based on acoustic recognition of neighbors: the so-called 'Dear Enemy' effect. In many species across taxa, it has been demonstrated that territorial neighbors show less aggression towards each other than they do towards strangers. For species that learn to sing during a short period of early life such as the zebra finches, it is possible to record in the laboratory all sounds produced during song ontogeny and to document moment-to-moment

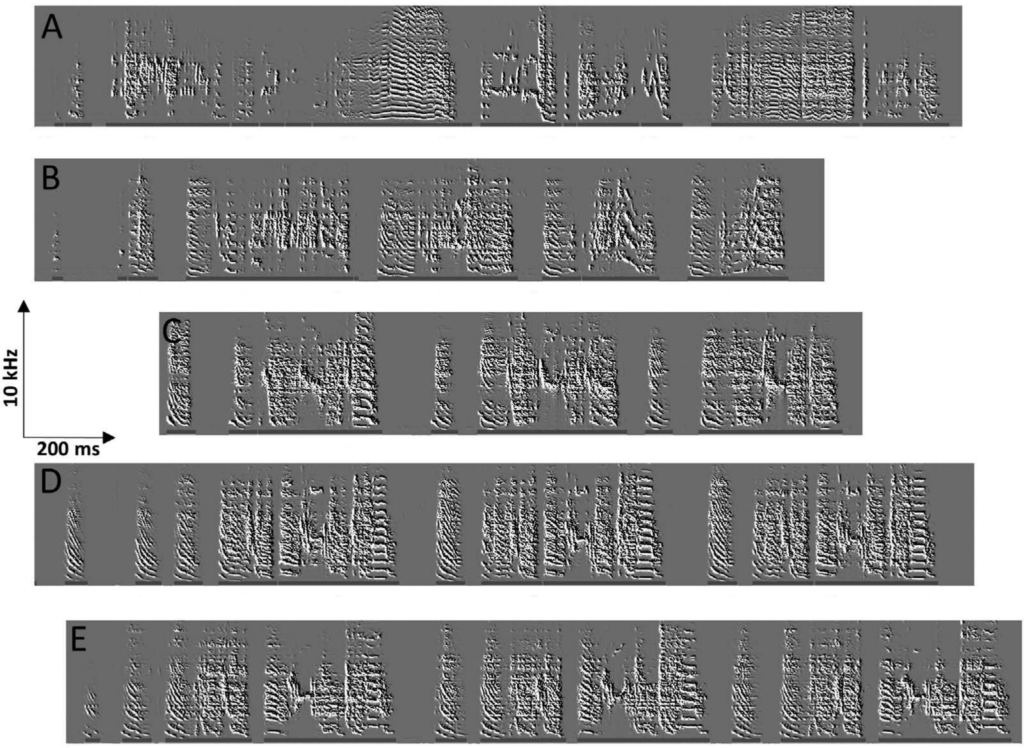

Figure 4.2 Song ontogeny in the Zebra Finch (*Taeniopygia guttata*). A–D: spectrograms of songs produced by a young male zebra finch during the sensitive period of song learning. A: first songs produced by the bird before exposure to an adult song tutor ("*subsong*"). B–C: two exemplars of the so-called "*plastic*" songs produced a few days after being exposed to the adult song tutor. D: adult version of the song, usually defined as "*crystallized*" song. E: spectrogram of the song produced by the adult tutor: note the high similarity with the adult song produced by the pupil.

changes. During periods of rapid learning, the song structure strongly deteriorates after night-sleep. Intriguingly, birds that showed a stronger post-sleep deterioration during development achieved a better final imitation of the playback song. Additional experiments showed that song deterioration was due to sleep (Derégnaucourt et al. 2005) and that brain plasticity during night sleep measured as dentritic spine turnovers could predict birdsong learning accuracy (Roberts et al. 2010).

In the zebra finch, several factors may affect the song learning process. Among them, the nutritional stress hypothesis has probably received the most emphasis. This hypothesis suggests that early life conditions, such as food provisioning (quantity, quality of food) or clutch sizes affect the song learning outcomes. Up to date, studies have shown mixed results (see Derégnaucourt 2011 for a review). Another hypothesis proposed that song learning reflects general cognitive abilities but again, while it was intensively tested, a recent literature review suggests that this is not the case (Searcy and Nowicki 2019). In recent studies, Mets and Brainard (2018; 2019) used both cross-fostering and computerized instruction with synthetic songs to demonstrate that matching the tutor song to individual predispositions can improve learning across genetic backgrounds in the Bengalese finch. First, they observed that inter-individual differences in song tempo have a strong genetic background: young birds tend to sing at the same tempo as their fathers, even if they have never heard their fathers' song (Mets and Brainard 2018). Second, they used a computerized tutoring program to train young finches with a tutor song that captured the average song structure and tempo found in their colony. They found that only birds from families singing at this intermediate tempo were able to learn this song model effectively, while birds with a family history of singing faster or slower songs did not succeed in learning accurately. In contrast, when finches were trained with a synthesized tutor song tailored to their genetic background (e.g. slower-tempo songs for birds from slow-singing families, higher tempo for birds from fast-singing families), they produced a good copy of the song model (Mets and Brainard 2019). This study demonstrates the importance of matching instruction to genetics; an important topic that could fuel reflections on the adaptation of educational programs in humans.

If birdsong ontogeny became such an important topic in behavioural biology, it is also because it represents a tractable model to measure the cellular and molecular substrates of vocal learning. Both human speech acquisition and birdsong learning show similarities in the architecture of their underlying brain areas, characterized by cortico-striato-thalamic loops and direct projections from cortical neurons onto brainstem motor neurons that control the vocal organs. In oscine songbirds, the pathways involved in sensorimotor integration of this learned behaviour belong to the so-called "song control system" (Nottebohm et al. 1976). Neural analogies extend to the molecular level, with some song control regions sharing convergent transcriptional profiles with speech-related regions in human (Aamodt et al. 2020). Using reversible and irreversible lesions in the songbird brain, electrophysiological recordings, sacrifice of animals at different stages of birdsong ontogeny and more recently genetic transfections and *in vivo* brain imaging, a considerable amount of data was accumulated over the last 50 years regarding parallel changes in developing behaviour and brain structure. In several oscine songbirds, seasonal changes in song structure are highly correlated with changes in testosterone levels (Nottebohm et al., 1987), which are accompanied by gross anatomical and cyto-architectural restructuring of the song control system (Vellema et al. 2014). In particular, since the pioneering works of Fernando Nottebohm (1981) showing that song changes in canaries occur concurrently to neurogenesis, hundreds of studies investigated how young neurons are born, migrate and are integrated in neuronal pathways linked to birdsong production and learning, even in adult birds. At the molecular level, using genetic transfection, the expression of the gene FOXP2 could be downregulated during the learning process in a specific brain area (area X) involved in song learning. This resulted in an incomplete and inaccurate imitation of the tutor song in zebra finches (Haesler et al. 2007). In humans, mutations affecting FOXP2 cause a rare form of severe speech and language disorder. More recently, there was significant progress in songbird transgenics with the goal of using birdsong learning as a model for human diseases (Aamodt et al. 2020). Germline transgenic songbirds expressing the human mutant huntingtin (mHTT), a protein responsible for the progressive deterioration of motor and cognitive function in Huntington's disease (HD), were developed. Although generally healthy, the mutant songbirds had severe vocal disorders, including poor vocal imitation, stuttering, and progressive syntax and syllable degradation (Liu et al. 2015). This integrated approach may thus be very informative.

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5

SENSATION, PERCEPTION, AND ATTENTION

Jessica L. Yorzinski and Will Whitham

Nearly fifty years ago, philosopher Thomas Nagel famously asked "What is it like to be a bat?" (Nagel 1974). To better understand "what is it like?", we would want to know what sensory information an individual has access to (sensation) and how this information is interpreted by the species (perception). Furthermore, we would want to understand why the species selectively processes some information while ignoring other information (attention). Our knowledge of the sensory and perceptual worlds of animals is growing rapidly, giving us greater insight into "what it is like" to be a bat or any other animal. This chapter will provide a broad overview of sensation, perception, and attention across diverse species. It will then discuss three case studies that highlight the importance of visual attention in guiding behaviour.

Comparative Sensation & Perception

Sensation is the process that allows species to access information from their environment. The core component of sensation is transduction: translating the environment, via sensory systems, into a form on which the brain can act. Perception is the cognitive process that interprets this sensory information. Both sensory and perceptual systems vary widely across species, and this can influence both what information each species has access to and how that information is interpreted. By studying the sensory and perceptual systems of diverse species, we can gain a deeper understanding of the forces shaping the evolution of these systems.

The visual system allows animals to see electromagnetic radiation, or energy that is reflected within their environments (Cronin et al. 2014). Photoreceptors within eyes are sensitive to specific wavelengths of electromagnetic radiation, and this influences what animals can see (Baden et al. 2020). Humans and many other animals see wavelengths within the visible spectrum, ranging from approximately 380 nm (violet) to 750 nm (red). In contrast, some animals can detect wavelengths below or above this range. Sensitivity to ultraviolet radiation, which includes short wavelengths between approximately 300 nm to 400 nm, is typical of many birds, fishes, reptiles, amphibians, and insects (Donner and Yovanovich 2020; Osorio 2019; van der Kooi et al. 2021). Some species, such as common lizards (*Zootoca vivipara*), bullfrogs (*Lithobates catesbeianus*), and zebrafish (*Danio rerio*), can detect wavelengths above the visible spectrum into the near-infrared (Martin et al. 2015; Enright et al. 2015). Because of these differences in visual sensitivities across species, an individual can appear markedly different depending on the species viewing it. For example, a male Northern swordtail fish (*Xiphophorus nigrensis*) has ultraviolet markings on its body that are highly visible (and attractive) to female conspecifics but relatively inconspicuous to one of its top predators (Cummings et al. 2003).

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Animals primarily detect sounds—vibrations that move through a medium such as air, water, or substrate—using their auditory system. Mechanoreceptors, such as hair cells and hair sensilla, typically transduce sounds by bending or stretching hair-like structures that then trigger nerve impulses (Bradbury and Vehrencamp 2011). Just as species vary in their visual sensitivities, species also vary in their sensitivity to specific sound frequencies. Humans generally hear frequencies that range from 20 to 20,000 Hz. Other species can hear frequencies above (ultrasound) or below (infrasound) this human hearing range. Bats are famous for hearing high frequencies (Arch and Narins 2008), while elephants are well-known for their ability to sense extremely low frequencies (Heffner and Heffner 1980). Because of interspecific differences in hearing sensitivities, animals do not always hear the same sounds. For example, Richardson's ground squirrels (*Spermophilus richardsonii*) emit ultrasonic alarm calls that nearby conspecifics can hear but many of their predators cannot (Wilson and Hare 2004).

The chemosensory system permits animals to detect chemicals through olfaction (smell) or contact (taste). Olfactory receptors detect chemicals in the air or water that originate from distant sources, while contact receptors detect chemicals by touching the original sources (Bradbury and Vehrencamp 2011). These chemoreceptors are generally activated by a variety of chemicals in a combinatorial manner but some can only be activated by specific chemicals (Touhara and Vosshall 2009). Similar to species differing in their visual and auditory sensitivities, species exhibit variation in their olfactory detection thresholds (Wackermannová et al. 2016). Dogs (*Canis lupus familiaris*) can often detect chemicals with substantially greater sensitivity compared with humans. For example, dogs can smell an acetate compound with concentrations as low as 1.14 parts per trillion, while humans can only detect that same compound when its concentration is above 7.11 parts per billion (Walker et al. 2003; Walker et al. 2006). Nevertheless, humans may actually have better developed olfactory systems than previously believed, as evidenced by humans' ability to track scents with high proficiency (Porter et al. 2007).

Many other sensory and perceptual systems exist across species, including some that are very different from human sensory systems. For example, electroreception is one such system that enables animals to detect electrical fields. Animals can use electroreception to locate prey (Kimber et al. 2014), as well as communicate with each other (Nagel et al. 2018). Many migratory species use magnetoception to successfully navigate thousands of miles by sensing the Earth's magnetic field (Naisbett-Jones et al. 2017). Other species rely strongly on their somatosensory system, as exemplified by naked mole-rats' (*Heterocephalus glaber*) reliance on touch to locomote through their dark underground tunnels (Crish et al. 2003).

While sensory and perceptual systems can vary across species, many of these systems can also vary within species. In white-faced capuchins (*Cebus capucinus imitator*), some females have trichromatic vision (three different photoreceptors) whereas other females and all males have dichromatic vision (two different photoreceptors; Hiramatsu et al. 2005). Capuchins with trichromatic vision find and consume more conspicuous fruits in the wild than their dichromatic counterparts, suggesting that polymorphic color vision may have evolved to enhance specific foraging strategies (Melin et al. 2017). Sensory and perceptual systems can even change over time within individuals. Sight, hearing, smell, or taste can decline over the course of typical aging in both humans and nonhuman animals (Townes-Anderson et al. 1998; Cavazzana et al. 2018). Sensory and perceptual systems can even change within individuals based on diet and seasonality. For example, the color vision sensitivity of birds is partly determined by pigment-rich oil in their eyes and this oil is influenced by their diet, suggesting that nutrition contributes to visual perception (Knott et al. 2010; Caves et al. 2020). Similarly, female plainfin midshipman fish (*Porichthys notatus*) have increased sensitivity to sounds during the breeding season, a time during which they choose among competing calls of potential mates (Sisneros 2009).

Rather than operating in isolation, sensory and perceptual systems interact with each other. Humans are better at detecting speech when they can both see *and* hear the speaker talking, compared to only hearing the speaker (Grant and Seitz 2000). Female túngara frogs (*Physalaemus pustulosus*) incorporate both auditory and visual information into their perception of male attractiveness (Taylor et al. 2008): females are more attracted to males that exhibit both a visual (vocal sac inflation) and auditory (whine-chuck call) component, rather than only an auditory component (whine-chuck call without vocal sac inflation). Because male frogs often emit calls when thousands of other males are simultaneously calling, the visual component may assist female frogs in correctly identifying their preferred mating partner.

The diversity of sensory and perceptual systems reflects the selective pressures imposed by the environment. Some species, like corals and anemones, have no need for detailed vision and have therefore evolved simple eyes rather than more complex ones (Picciani et al. 2018). Many sensory and perceptual systems have evolved independently in disparate species because of convergent needs for those systems. As a case in point, blue tits (*Cyanistes caeruleus*) and chestnut tiger butterflies (*Parantica sita*) have eyes with color vision and sensitivity into ultraviolet ranges, but their eyes vary widely in overall structure (blue tits have lens eyes and chestnut tiger butterflies have compound eyes) and visual pigments (Hart et al. 2000; Nagloo et al. 2020) since they evolved independently. Because sensory and perceptual systems are costly to develop and maintain, natural selection would not favor individuals investing in systems that do not contribute to survival or reproduction. It is for this reason that some sensory and perceptual systems have been lost over evolutionary time. For example, vision has been lost in species that do not need it: obligate cave-dwelling species spend their entire lives in the dark and can no longer see even though their ancestors were capable of sight (Stern and Crandall 2018).

Understanding sensory and perceptual systems from a comparative perspective is of particular importance given the growing impact of anthropogenic disturbances (i.e., human impacts on the environment). Light pollution at night is a common anthropogenic disturbance that is increasing globally and it can drastically alter the lighting environment that animals are exposed to (Kyba et al. 2017). The sleep patterns of many species, including birds and mammals, are disrupted by light pollution at night, with many species perceiving days as longer than they actually are (Dominoni and Partecke 2015; LeTallec et al. 2015). However, the effect of light pollution is not necessarily uniform across species: light pollution does not affect sleep in a species of cavity-nesting birds, potentially because the cavity shields individuals from light pollution (Raap et al. 2018). Noise pollution is another common anthropogenic disturbance, and it has the potential to mask biologically relevant sounds. Great tits (*Parus major*) are unable to detect alarm calls when traffic noise is loud; as a result, these birds do not exhibit appropriate antipredator behaviour in response to alarm calls and potentially suffer higher predation rates (Templeton et al. 2016). Individuals can sometimes adjust to these anthropogenic disturbances, through behavioural or even genetic mechanisms, but it is still unclear what the long-term consequences of these adjustments might be (Read et al. 2014; Hamilton et al. 2017). Additional research that examines the impacts of anthropogenic disturbances on sensory and perceptual systems will be increasingly valuable in guiding conservation efforts (Blumstein and Berger-Tal 2015).

Comparative Attention

Animals have access to an abundance of information—both information about their immediate surroundings obtained by their sensory and perceptual systems, as well as previous information retained in learning and memory. Due to cognitive limitations, it is impossible for any animal to sense and process all of this information at once. Attention functions to direct cognitive processing to a subset of this vast array of information, guiding sensory and perceptual systems to information that is most relevant to the current task.

Attention is often driven by both bottom-up and top-down processes (Katsuki and Constantinidis 2014). Bottom-up (lower-level) processes guide attention exogenously by properties of the stimuli. Visual attention is often attracted toward certain colors and shapes (Itti and Koch 2001) while auditory attention is often attracted toward loud sounds (Kaya and Elhilali 2014). In contrast, top-down (higher-level) processes direct attention toward task-relevant stimuli (Shinoda et al. 2001). As an example, the visual attention of a monkey may be drawn by the initial movement of a predator (bottom-up process) and then sustained because the predator is recognized as a threat (top-down process). Through both bottom-up and top-down processes, animals can selectively direct their attention toward information that informs their behavioural decisions while ignoring distracting information.

Animals often vary in where they direct their attention because the salience of information differs across individuals and species. Female frogs simultaneously hear thousands of male advertisement calls that humans may perceive as an extremely dense chorus of overlapping sounds. The female frogs, however, can focus their attention on the particular calls needed to make their reproductive decisions (Bee 2012). Animals can also vary in where they direct their attention over the course of development. When attempting to use a stone hammer to crack a nut, juvenile capuchin monkeys (*Sapajus [Cebus] libidinosus*) attend excessively to relatively irrelevant properties of the nut (e.g., its smell and the sound it makes when knocked against a hard surface), in ways that adult capuchin monkeys do not (Fragaszy et al., 2020).

Through a discussion of three case studies across diverse species (humans, Indian peafowl, and jumping spiders), we illustrate how animals selectively direct their visual attention toward information that is important for informing their decisions. In each case study, eye-trackers were used to monitor where the animals were gazing within their environments (Figure 5.1). The eye-trackers monitored the retinal region of each species that had the highest spatial acuity and determined where each retinal region was directed within the visual field. They tracked the fovea and area centralis in humans and Indian peafowl (*Pavo cristatus*), respectively, while tracking the center of the boomerang-shaped retinas in jumping spiders (*Phidippus audax*; Land 1969; Hart 2002). Eye-trackers are powerful tools that continuously record where animals are directing their overt attention, and can therefore help us understand how selective attention is used to inform behavioural decisions across diverse species. These case studies highlight the important role that visual attention plays across varied contexts including locomotion, courtship, and predation.

Figure 5.1 An eye-tracker records the gaze of a (left) person (photo prepared by Jon Matthis, Department of Biology, Northeastern University), (middle) peahen (photo prepared by Jessica Yorzinski), and (right) spider (photo prepared by Gui Pagoti and Beth Jakob, Department of Biology, University of Massachusetts at Amherst). The person and peahen are wearing mobile eye-trackers that consist of camera systems to monitor their gaze as they freely move within their environments. The spider is reversibly tethered by its cephalothorax and positioned so that she is looking into the eye-tracker and viewing the stimuli.

Case Study: Locomotion

Visual attention is a critical component of successful locomotion for many species. Individuals need to selectively direct their attention toward aspects of their environments that will enable them to safely locomote. When individuals fail to properly move within their environment, they risk injury and potentially even death. Humans are particularly reliant on visual information when they walk along terrain of varying complexity (Matthis et al. 2018). When walking over complex terrain (small rocks scattered among loosely-packed soil or large rocks scattered among small rocks), humans spend most of their time gazing at the ground: they are primarily looking two or three steps ahead of their current position (Figure 5.2). By looking ahead, humans can plan their future steps while maximizing gait performance. In contrast, when walking over simple terrain (flat, compacted soil), humans only look at the ground about half of the time. Because the simple terrain has few obstacles, humans do not need to devote as much time to planning their future steps and can instead direct their attention toward other aspects of the environment. Humans therefore use gaze strategies during locomotion that balance their needs of maintaining stability while efficiently moving within environments of varying complexity. Selective attention likely plays a fundamental role during locomotion in many other species and additional research into this topic could reveal how diverse species successfully locomote while simultaneously performing other tasks (such as monitoring predator movements while running over complex terrain).

Case Study: Courtship

Visual attention plays a crucial role in sexual selection. Many individuals rely on visual information to assess their mating partners as well as their competitors (Andersson 1994). This visual information can indicate the health, social status, reproductive quality, physical condition or other qualities of mating partners and competitors (Bateson and Healy 2005). Individuals must selectively direct their attention toward relevant aspects of their potential mates or competitors in order to extract the information they need to inform their mating and agonistic decisions. Visual attention is particularly important during female mate choice and rival assessment in peafowl (Yorzinski et al. 2013, 2017). Peafowl are icons of sexual selection, with peacocks displaying elaborate traits that both females and males assess. Rather than directing their gaze uniformly across the peacocks' traits during courtship, peahens primarily gaze at the lower portions of the peacocks' trains (Figure 5.2, 5.3): potentially

Figure 5.2 (left) A human is directing his gaze (indicated by the crosshair) toward the complex terrain as he walks over it. The eye insets show the eye positions that were used to generate the gaze position (photo prepared by Mary Hayhoe). (middle) A peahen is directing her gaze (indicated by the crosshair) toward a displaying peacock during the mating season. The eye inset shows the eye position that was used to generate the gaze position (photo prepared by Jessica Yorzinski). (right) A jumping spider is directing her gaze (indicated by the center of the boomerang-shaped retinas) toward a cricket.

(Photo prepared by Beth Jakob, Department of Biology, University of Massachusetts at Amherst).

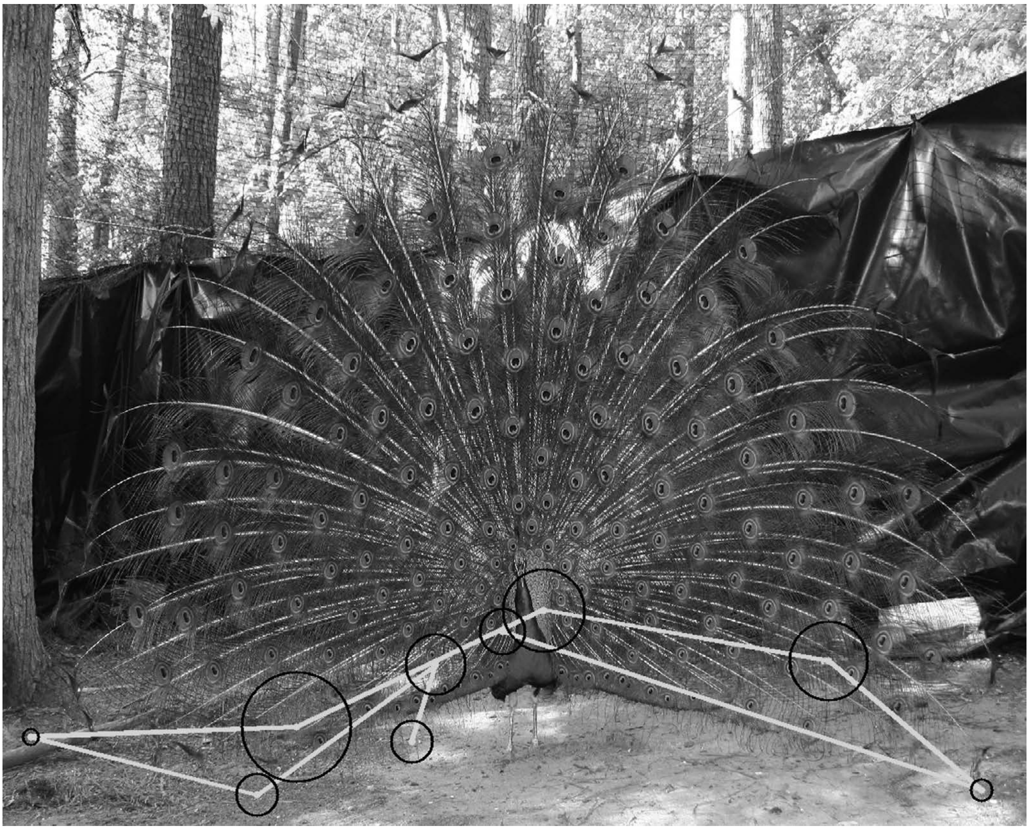

Figure 5.3 Scanpath of a peahen evaluating a displaying peacock during the mating season; the size of the circles represents the amount of time the peahen looks at each location (photo prepared by Jessica Yorzinski).

assessing their width, symmetry, or number of eyespots. Consistent with these gaze patterns, peahens often mate with males that have long trains and a large number of eyespots (Manning 1987; Petrie and Halliday 1994; Loyau et al. 2005; Dakin and Montgomerie 2011). In addition, peacocks sometimes rattle their feathers during courtship, and this behaviour captures and maintains the peahens' attention. Similarly, peacocks also selectively direct their attention toward their competitors: they mainly gaze at the lower portion of their competitors' trains. Given that peacocks with longer trains are more successful against their rivals (Loyau et al. 2005), it would be important for males to visually evaluate the relevant aspect of their rivals' trains to extract this information. Selective attention is clearly important during sexual selection in peafowl and likely influences the evolution of male display traits. Further studies examining the role of selective attention could reveal common factors that attract attention during courtship across species.

Case Study: Predation

Visual attention is often involved when predators capture their prey. These predators must selectively direct their attention within their environments to locate potential prey and then attack them. They can use a variety of visual features, such as color, size, and motion, to accomplish this. Jumping spiders are predators that are well-known for their superior visual capabilities: they have four pairs of eyes that include two principal eyes and two antero-lateral eyes (Land 1969; Morehouse et al. 2017). The two principal eyes have a narrow field of view but high spatial acuity while the antero-lateral eyes have a wide field of view but lower spatial acuity. When potential prey appear within their visual field, jumping spiders can selectively direct their attention toward the prey by moving their principal eyes toward them (Figure 5.2). However, their ability to do so is limited when their antero-lateral eyes are masked. When their antero-lateral eyes are masked, the principal eyes cannot find the prey unless the prey appear directly in front of the principal eyes. The antero-lateral eyes are therefore essential to locating prey within the entire visual field and alerting the principal eyes to the specific location of the prey (Jakob et al. 2018). Furthermore, the antero-lateral eyes remain important even when the principal eyes have located the prey. The antero-lateral eyes can detect potential threats in the environment when the principal eyes are focused on the prey, causing the principal eyes to shift their attention from the prey towards imminent danger (Bruce et al. 2021). Selective attention, guided by both sets of eyes, is critical for these predators to successfully locate and track their prey as well as avoid threats. Understanding how predators employ selective attention to find camouflaged prey could be a particularly promising area for additional research.

Limitations of Attention

While attention is necessary for processing information within complex environments, it is important to note that limitations of attention can restrict sensation and perception. In particular, many species can simultaneously attend to multiple stimuli or tasks ('divided attention'), but they often do so at a cost. When blue jays (*Cyanocitta cristata*) searched for two different prey types (during a computerized task on which they were trained), they detected fewer prey compared to when they searched for only a single prey type (Dukas and Kamil 2001). Similarly, salmon (*Salmo salar*) are least efficient in foraging when they are simultaneously at high risk of predation (Metcalfe et al. 1987). Because animals are focusing their attention on a subset of stimuli in their environments, they can also potentially miss important information. For example, when humans are counting the number of times basketball players pass the ball, they often fail to notice a person dressed in a gorilla costume walking near the players ('inattentional blindness'; Simons and Chabris 1999). Pigeons (*Columba livia*) likewise do not always notice major changes in their visual environment ('change blindness;' Herbranson et al. 2014). We still have much to learn about how these limitations in attention influence sensation and perception, especially in nonhuman species.

Conclusion

We have provided a general overview of sensation, perception and attention across phylogenetically diverse species. Sensory and perceptual systems can vary both within and among species, and these systems have evolved to meet specific needs that enhance survival and reproduction. Attention interacts with these sensory and perceptual systems so that animals can focus on relevant information. While we are closer to understanding "what it is like" to be a bat or any other animal, we still have much to uncover. Future research that further probes the sensory and perceptual systems of diverse species will surely yield fascinating discoveries that will build our understanding of how animals experience the world.

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6

MOTIVATION AND EMOTION

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Introduction

The word *motivate* means 'to cause to move', and I will use the concept of motivation to refer to the study of the immediate causes of behaviour: those factors responsible for the initiation, maintenance, and termination of behaviour. Causal factors for behaviour include stimuli, hormones, and the intrinsic activity of the nervous system. How do these factors cause a female rat to behave maternally to her pups? Or a chicken to bathe in dust in the middle of the day? Or a male stickleback fish to stop responding sexually to receptive females? These are the types of questions asked in the first part of this chapter.

Motivated behaviour often produces emotion, but the concept of emotion is problematic because there is no consensus about its definition. In the second part of this chapter, I will analyze the concept of emotion as applied primarily to humans and conclude with a section on non-human emotion and its relation to animal welfare.

A major problem in the study of both motivation and emotion is that different authors use these concepts in different ways. Causal factors not only motivate behaviour, but also they can change the structure of behaviour; that is, they have developmental effects. The formation of associations and the effects of reinforcement are developmental processes, and developmental processes have played an important role in many theories of motivation, especially in experimental psychology (see Hogan, 1998). In this chapter, however, I will restrict the term motivation to the modulating effects causal factors have on the activation of behaviour systems. Development refers to the permanent effects causal factors have on the structure of behaviour systems, and is discussed in Chapter 4. Emotion is considered to be one of the consequences of activating behaviour mechanisms and will be discussed later.

Causal Factors

Stimuli

Stimuli can control behaviour in many ways: they can release, direct, inhibit, and prime behaviour. The reproductive behaviour of the three-spined stickleback (*Gasterosteus aculeatus*), a small fish, provides many examples of these functions of stimuli (Tinbergen, 1951). Male sticklebacks set up territories in small streams early in the spring, build a nest of bits of plant material, and will generally court any female that may pass through their territory. Courtship includes a zigzag dance by the male, appropriate posturing by the female, leading to and showing of the nest entrance by the male, following and entering the nest by the female, laying eggs, and finally fertilization. The female swims away and the

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male then courts another female. It is the behaviour of the female that releases and directs the courtship movements of the male, and the behaviour of the male that releases and directs the courtship movements of the female.

The male could continue courting egg-laden females for many days, but usually he does not. Experiments in which eggs were removed from or added to the nest have shown that visual stimuli from the eggs inhibit sexual activity: if eggs are removed from the nest, the male will continue courting females, but if eggs are added to the nest he will cease courting, regardless of the number of eggs he has fertilized (Sevenster-Bol, 1962). This is an especially interesting example because the same stimulus that inhibits sexual activity also stimulates parental behaviour.

In the stickleback, both the visual stimulus of eggs in the nest and CO_2 from the eggs, which increases as the eggs develop, release parental (fanning) behaviour. Fanning directs a current of water into the nest and serves to remove debris and provide oxygen to the developing embryos. The amount of fanning increases over the seven days it takes for the eggs to hatch. Experiments have shown that removing old eggs from the nest after four days, and replacing them with fresh eggs, thus lowering the CO_2 level but leaving the visual stimulus unchanged, does not reduce fanning behaviour substantially, and that fanning behaviour reaches a peak on day 7 when the original eggs would have hatched (van Iersel, 1953). This means that the stimuli from the eggs must prime a coordinating mechanism, and that the state of the coordinating mechanism is no longer completely dependent on stimulation from the eggs after three or four days.

When a stimulus has arousing effects on behaviour that outlasts its presence, 'priming' is said to occur. In the case of the stickleback, priming of parental behaviour occurs over the course of several days. In other cases, priming occurs over the course of a few minutes. Aggressive behaviour in the male Siamese fighting fish (*Betta splendens*) provides a good example (Hogan & Bols, 1980). This fish shows vigorous aggressive display and fighting toward other males of its species (including its own mirror image). If a fish is allowed to fight with its mirror image for a few seconds and the mirror is then removed, it is very likely to attack a thermometer introduced into the aquarium. If the thermometer had been introduced before the mirror was presented, the fish very likely would have ignored it. Thus, the sight of a conspecific not only releases aggressive behaviour, it must also change the internal state of the fish for some time after the conspecific disappears. We can say that the stimulus primes the mechanism that coordinates aggressive behaviour or, more simply, that it primes aggression. Similar priming effects have been demonstrated with food and water in rats and hamsters, and with brain stimulation in several species (see Hogan & Roper, 1978). An especially elegant mathematical analysis of priming in cichlid fish and crickets is presented by Heiligenberg (1974).

Even longer-term motivational effects of stimuli can be seen in the yearly cycle of gonad growth and regression in some birds and fish as a result of changes in day length. And changes in day length can also stimulate a host of other physiological changes including those that prepare migratory birds for their long-distance flight (e.g., Piersma & van Gils, 2011) or various mammals for hibernation in the winter (Nelson, 2016).

Hormones and other substances

Hormones are substances released by endocrine glands into the bloodstream; many of them are known to have behavioural effects (Balthazart & Ball, 2022). Both peripheral and central effects of the hormone prolactin are seen, for example, in the parental feeding behaviour of the ring dove (*Streptopelia risoria*). Prolactin is responsible for the production of crop 'milk', sloughed-off cells from the lining of the crop that are regurgitated to feed young squabs. Lehrman (1955, 1965) hypothesized that sensory stimuli from the enlarged crop might induce the parent dove to approach the squab and regurgitate. His experiments showed that local anesthesia of the crop region, which removes the sensory input, reduced the probability that the parents will feed their young. The maternal behaviour of the rat provides an example that illustrates the variety of hormonal effects. The hormones released at parturition change the dam's olfactory sensitivity to pup odors, reduce her fear of the pups, and facilitate learning about pup characteristics; they also activate a part of the brain essential for the full expression of maternal behaviour (see Fleming & Blass, 1994).

Hormones also play an essential role in the motivation of aggressive and sexual behaviour in most species, as well as in reactions to stress. Other substances, released from the neuron terminals into the synapse, known as neurotransmitters, are involved in activating specific behaviour systems such as feeding and drinking (see Nelson, 2016). The transmitter dopamine is thought to mediate the motivational effects of stimuli for a wide range of behaviour systems, especially their reinforcing effects (Glimcher, 2011). Psychoactive drugs are also thought to exert their effects by altering neurotransmitter functioning in the brain.

Intrinsic neural factors

In living organisms, the nervous system is continuously active, and this has many consequences for the occurrence of behaviour. That behaviour can occur spontaneously, i.e. without any apparent external cause, was an idea that was long resisted by many behavioural scientists. However, it has gradually become clear that intrinsic causes can be studied scientifically, and that any explanation of behaviour that only takes the effects of external stimuli into account will be incomplete.

The motivational model of Lorenz (1950) was an early attempt to incorporate intrinsic factors as a cause of behaviour. Lorenz postulated that the motivational energy for a particular behaviour pattern builds up as a function of time since its last occurrence. He metaphorically represented motivational energy as fluid in a reservoir. Such a model can account reasonably well for the behaviour of some systems (e.g. hunger and thirst), but not so well for systems such as sex and aggression that are primarily externally motivated. Its generality can be increased, however, if the motivating effects of priming can be included in the reservoir (Hogan, 1997).

Lorenz's model implies a continuously active nervous system kept in check by various kinds of inhibition (hence, releasing mechanisms). A particularly striking example concerns the copulatory behaviour of the male praying mantis (*Mantis religiosa*). Mantids are solitary insects that sit motionless most of the time waiting in ambush for passing insects. Movement of an object at the correct distance and up to the mantis's own size releases a rapid strike. Any insect caught will be eaten, even if it is a member of the same species. This cannibalistic behaviour might be expected to interfere with successful sex, because the male mantis must necessarily approach the female if copulation is to occur. Sometimes a female apparently fails to detect an approaching male and he is able to mount and copulate without mishap, but very often the male is caught and the female then begins to eat him. Now an amazing thing happens. While the female is devouring the male's head, the rest of his body manages to move round and mount the female, and successful copulation occurs.

In a series of behavioural and neurophysiological experiments, Roeder (1967) showed that surgical decapitation of a male, even before sexual maturity, releases intense sexual behaviour patterns. He was then able to demonstrate that a particular part of the mantis's brain, the subesophageal ganglion, normally sends inhibitory impulses to the neurons responsible for sexual behaviour. By surgically isolating these neurons from all neural input, he showed that the neural activity responsible for sexual activity is truly endogenous.

A more recent example of endogenous control is dustbathing behaviour in fowl. Most animals possess behaviour patterns that can be used for cleaning themselves or for keeping their muscles, skin, or feathers in good condition. These patterns range from simply stretching or rubbing up against some object to complex integrated sequences of behaviour used for grooming in many species, such as dustbathing in fowl. This behaviour comprises a sequence of coordinated movements of the wings, feet, head, and body of the bird that serve to spread dust through the feathers. One might suppose that this behaviour is primarily a reaction to dirt or parasites on the feathers or skin. However, a series of

Figure 6.1 Genetically featherless chicks dustbathing in sand.

Courtesy of Klaus Vestergaard.

experiments, testing young chicks after periods of dust deprivation, has provided strong evidence that dustbathing is primarily endogenously controlled. In one experiment it was possible to test genetically featherless chicks (see Figure 6.1); these chicks also showed a strong correlation between length of dust deprivation and amount of dustbathing, even though the chicks' bodies were thoroughly cleaned prior to testing (Vestergaard et al., 1999).

The intrinsic factors just discussed are all related to the motivation of specific behaviour patterns. One additional intrinsic factor is the pacemaker or oscillator cells that are thought to be responsible for biological clocks (Mistleberger & Rusak, 2022). These clocks do not control any specific behaviour pattern, but rather modulate the behaviour mechanisms that control many different types of behaviour. Dustbathing in chickens again provides an example. A bout of dustbathing can last for half an hour and usually occurs in the middle of the day (Vestergaard, 1982). Experiments have confirmed that the timing of dustbathing is controlled by an internal circadian clock (Hogan & van Boxel, 1993). The timing of human sleep is also an important example of oscillator control of behaviour (Borbély et al., 2001).

There are many other examples of oscillator control of behaviour. Most of the experimental work has investigated the oscillators responsible for daily (circadian) rhythms, often at a neurophysiological or genetic level, but there has also been considerable work on the oscillators controlling longer and shorter rhythms, as well as interval and hourglass timers (Buhusi & Meck, 2005).

Interactions among Behaviour Systems

Causal factors for many behaviour systems are present at the same time, yet an animal can generally only do one thing at a time. This is a situation of motivational conflict. The most common outcome in a conflict situation is that the behaviour system with the highest level of causal factors will be expressed and all the other systems will be suppressed. A male stickleback that is foraging in its territory will stop foraging when a female enters and will begin courting. The male's hunger has not changed, nor has the availability of food. It follows that the activation of the systems responsible for courtship must have inhibited the feeding system. In general, behaviour system inhibition can be said to occur when causal factors are present that are normally sufficient to elicit a certain kind of behaviour, but the behaviour does not appear as a result of the presence of causal factors for another kind of behaviour.

Sometimes inhibition of a behaviour system is not complete, and incipient movements belonging to the suppressed behaviour systems are seen. These provide an indication of the relative strength of the causal factors for other behaviours that are activated in the situation. They have been called ‘intention movements’ because they suggest to an observer, human or conspecific, what behaviour might occur next (see Chapter 10 on Communication herein).

Ambivalence

Ambivalent behaviour is behaviour that includes motor components belonging to two or more different behaviour systems. When a female stickleback enters the territory of a male, she is both an intruder and a potential sex partner. The appropriate response to an intruding conspecific is to attack it; the appropriate response to a sex partner is to lead it to the nest. The male essentially does both; he performs a zigzag dance: he makes a sideways leap followed by a jump in the direction of the female, and this sequence may be repeated many times. Sometimes the sideways leap continues into leading to the nest, and sometimes the jump toward the female ends in attack and biting. Thus, the zigzag dance can be considered a case of successive ambivalence.

Often, components belonging to different behaviour systems occur simultaneously. This greatly increases the number and variety of behaviour patterns in a species’ repertoire. A technique called ‘motivation analysis’ can be used to explore such ambivalent behaviour patterns, which include many of the bizarre displays exhibited by many species. In a motivation analysis, one looks at the form of the behaviour, the situation in which it occurs, and other behaviours that occur in association with it (Tinbergen, 1959).

An example is provided by Kruijt’s analysis of ‘waltzing’ by the male junglefowl (G*allus gallus spadiceus*), the wild ancestor of the domestic chicken (see Figure 6.2). It is a lateral display in which the male walks sideways around or toward the female. Kruijt noted that the side of the bird’s body near the hen expressed many components of escape behaviour, whereas the side further from the hen expressed many components of attack behaviour. It was “as if the part of the animal which is nearest to the opponent tries to withdraw, whereas the other half, which is further away, tries to approach” (Kruijt, 1964, p. 65). He also noted that waltzing was always directed toward a conspecific. Somewhat surprisingly, young males directed waltzing equally to males and females, even though adult males almost always direct it toward females. In about two-thirds of the cases it was performed immediately before, during, or immediately after fighting, and in some of these cases behaviour associated with escape was also seen. Thus, on the basis of form, situation, and associated behaviour, Kruijt could conclude that waltzing is indeed an ambivalent behaviour pattern expressing both attack and escape, with attack predominating. Sexual motivation appears to be unnecessary.

Motivation analysis of many complex courtship displays in both birds and mammals has revealed that they are ambivalent activities very frequently involving primarily the attack and escape systems. Such activities are usually essential for successful courtship and reproduction. This means that the sex system by itself is often insufficient for achieving these ends, and illustrates clearly why causal and functional questions need to be kept separate.

Displacement

Ambivalent behaviour and redirected behaviour are appropriate responses to causal factors that are obviously present in the situation in which the animal finds itself. Sometimes, however, an animal shows behaviour that is not expected, in that appropriate causal factors are not apparent. A male stickleback meets its neighbor at the territory boundary and shows intention movements of attack

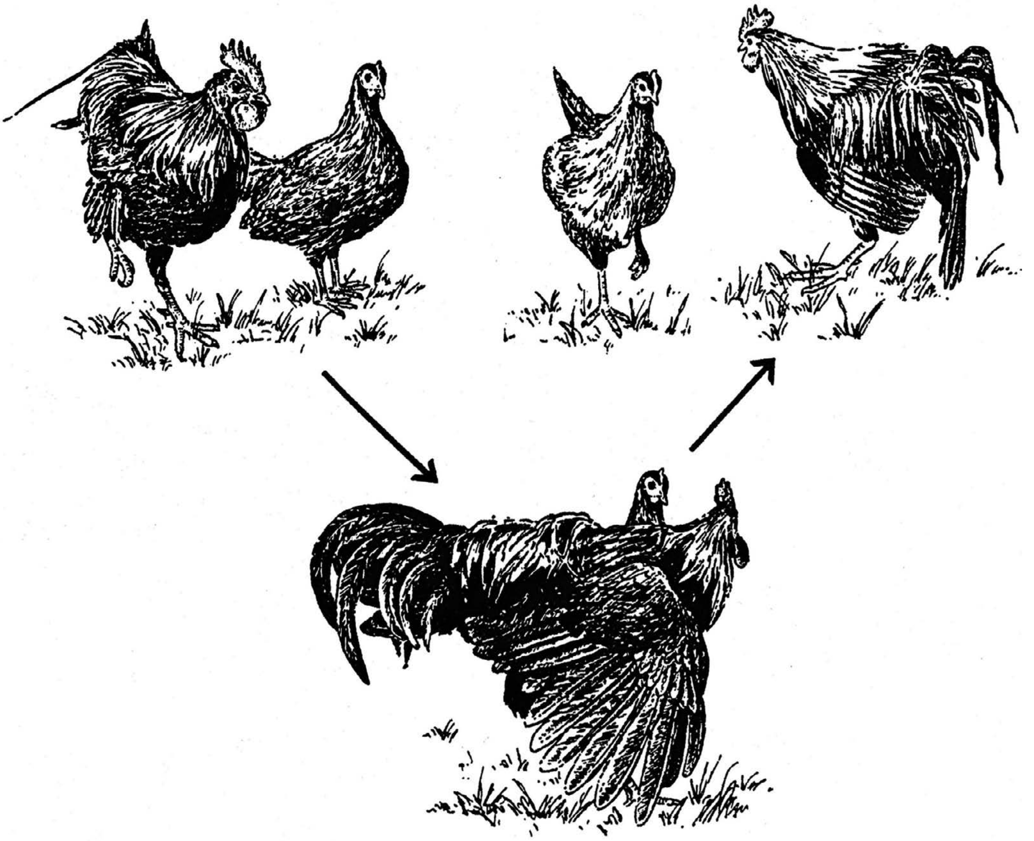

Figure 6.2 'Waltzing' in a male junglefowl.

Courtesy of Jaap Kruijt.

and escape; then it suddenly swims to the bottom and takes a mouthful of sand (which is a component of nest-building behaviour). A young chick encounters a wriggling mealworm and shows intention movements of approach to peck and eat the mealworm and of retreating from the novel object; then, while watching the mealworm the chick falls asleep (Hogan, 1965). A pigeon, actively engaged in courtship, suddenly stops and preens itself. These behaviours are all examples of 'displacement activities' that are controlled by a behaviour system different from the behaviour systems one might expect to be activated in a particular situation.

In the case of the stickleback, it is reasonable to show components of attack and escape behaviour at the boundary of its territory because the neighboring fish is a potential intruder. But why should it engage in nest-building behaviour? The stickleback has probably already built its nest elsewhere and, in any case, would not normally build it at the edge of its territory. What are the causal factors for nest building in this situation?

Two main theories have been put forward to account for displacement activities: the overflow theory and the disinhibition theory. The overflow theory was proposed independently by Kortlandt (1940) and by Tinbergen (1940). They proposed that when causal factors for a particular behaviour system (e.g., aggression) were strong, but appropriate behaviour was prevented from occurring, the energy from the activated system would 'spark' or flow over to a behaviour system that was not blocked (e.g., nest building) and a displacement activity would be seen. The appropriate behaviour might be prevented from occurring because of interference from an antagonistic behaviour system (e.g., fear or escape) or the absence of a suitable object or thwarting of any sort. This theory was formulated in the framework of Lorenz's model of motivation, which accounts for the graphic metaphor of energy sparking over or overflowing. In more prosaic terms, this is actually a theory in which causal factors have general as well as specific effects.

The alternative theory is called the disinhibition theory. In essence, it states that a strongly activated behaviour system normally inhibits weakly activated systems. If, however, two behaviour systems are strongly activated (e.g., sex and aggression) the inhibition they exert on each other will result in a release of inhibition on other behaviour systems (e.g., parental) and a displacement activity will occur. The general idea was proposed by several scientists, but the most detailed exploration of the theory was made by Sevenster (1961). He studied displacement fanning in the male stickleback, which often occurs during courtship before there are any eggs in the nest. The sex and aggression behaviour systems are known to be strongly activated during courtship. By careful measurements, it was possible to show that fanning occurred at a particular level of sex and aggression when their mutual inhibition was the strongest. Of special importance for the disinhibition theory, the amount of displacement fanning that occurred depended on the strength of causal factors for the parental behaviour system: when extra CO_2 was introduced into the water, there was an increase in displacement fanning.

Which theory is correct? As is so often the case, neither theory, by itself, is able to account for all the phenomena associated with displacement activities. The disinhibition theory is in many ways more satisfying because it only requires that causal factors have their normal and expected effects on behaviour. Nonetheless, more general effects of causal factors must be invoked to account for the frantic or excited aspects of displacement activities seen in many situations. The causation of behaviour is a very complex question, and it is unreasonable to expect a simple answer.

Mechanisms of Behavioural Change

What determines when a particular behaviour will occur, how long it will continue, and what behaviour will follow it? One can imagine that all an animal's behaviour systems are competing with each other for expression, perhaps in a kind of free-for-all, and that the system with the strongest causal factors would be expressed. Unfortunately, this account is clearly an oversimplification of reality. Perhaps its most serious shortcoming is that if there were a real free-for-all and only the most dominant behaviour system could be expressed, many essential but generally low-priority activities might never occur. Lorenz (1966) has compared the interactions among behaviour systems to the working of a parliament that, though generally democratic, has evolved special rules and procedures to produce at least tolerable and practicable compromises between different interests. The special rules that apply to interactions among behaviour systems have only begun to be studied, but a few principles are beginning to emerge.

One important mechanism for behavioural change arises from the fact that most behaviour systems are organized in such a way that 'pauses' occur after the animal has engaged in a particular activity for a certain time. The level of causal factors for the activity may remain very high, but during the pause other activities can occur. For example, in many species, feeding occurs in discrete bouts; between bouts there is an opportunity for the animal to groom, look around, drink, and so on. It appears that the dominant behaviour system (in this case, the hunger system) releases its inhibition on other systems for a certain length of time. During the period of disinhibition, other behaviour systems may compete for dominance according to their level of causal factors or each system may, so to speak, be given a turn to express itself.

A striking example of this sort of behavioural organization is the incubation system of certain species of birds. Broody hens sit on their eggs for about three weeks. Once or twice a day, the hen gets off the eggs for about 10 min. During this interval she eats, drinks, grooms, and defecates. The proportion of the 10 min spent eating will vary depending on the state of her hunger system, but even 24 h of food deprivation does not change the pattern of leaving the eggs (Sherry et al., 1980).

Another type of mechanism for behaviour change depends upon the reaction of an animal to discrepant feedback. A male Siamese fighting fish, for example, will not display as long to its mirror image as to another displaying male. This is because the behaviour of the mirror image is always identical to the behaviour of the subject, but identical responses are not part of the 'species expectation' of responses to aggressive display (Bols, 1977). These mechanisms, and undoubtedly many others, all interact to produce the infinite variety of sequences of behaviour characteristic of the animal in its natural environment.

(Human) Emotion

Emotion is one of the consequences of activating various behaviour mechanisms. But specifying the concept in more detail is problematic because there is no consensus about its definition. Books have been written on the subject (e.g., Ekman & Davidson, 1994; Barrett & Russell, 2015) and two major journals, *Emotion* and *Emotion Review*, publish studies on emotion. The term usually refers to certain subjective experiences called feelings, but observable features often accompany them. I have defined a feeling as the activation of a specific central behaviour mechanism (Hogan, 2017), but characterizing those behaviour mechanisms that subserve emotion is as intractable as the concept of emotion itself. I think some insight into the problem can be gained by considering some of the views of William James (1890, vol. 2):

> Our natural way of thinking about these coarser emotions [grief, fear, rage, love] is that the mental perception of some fact excites the mental affection called the emotion, and that this latter state of mind gives rise to the bodily expression. My theory, on the contrary, is that *the bodily changes follow directly the perception of the exciting fact, and that our feeling of the same changes as they occur* is *the emotion.*
>
> *(p. 449).*

In other words, when we meet a bear and run away, we are not running away because we are frightened; we are frightened because we are running away—fright is our perception of all the bodily changes that occur when we run away.

This theory has been subject to much criticism. Historically, the idea that has been most discussed is his idea that emotion *is* the perception of the feedback one gets from bodily changes in response to some arousing situation. Everyone agrees that most emotional situations cause a multitude of visceral changes such as increases in heart rate, vasoconstriction, sweating, etc., all of which are caused by sympathetic nervous system action. However, Cannon (1927) challenged the notion that perception of these changes is the emotion for several reasons. He pointed out that the viscera are relatively insensitive structures and that visceral changes are too slow to account for emotional feelings that occur demonstrably quicker. He also cited results of Marañon, who injected epinephrine, a sympathetic nervous system stimulant, into human subjects and asked them to describe their feelings. The results showed a clear distinction "between the perception of the peripheral phenomena of vegetative emotion (i.e. the bodily changes) and the psychical emotion proper, which does not exist and which permits the subjects to report on the vegetative syndrome with serenity, without true feeling" (tr. by Cannon, 1927, p. 113).

Schachter & Singer (1962) proposed that the quality of an emotion is arrived at by a process of cognitive appraisal. In one of their experiments, they also injected epinephrine into human subjects. Some of the subjects were told what effects they might expect and others were not told anything about the effects. All subjects were then observed in the presence of a confederate of the experimenter who acted in either an elated or angry manner. The subjects were later asked about their emotional reactions. The informed subjects reported very little emotion (as also the subjects of Marañon); but the uninformed subjects did report emotional feelings, and the kind of emotion they felt tended to mimic that of the confederate. In other words, in precisely the same state of physiological arousal, emotional labels depended on the cognitive aspects of the situation.

Since 1962, there have been hundreds of studies on emotion. Gendron & Barrett (2009) review the history of scientific ideas about emotion and posit three major approaches to its study: basic emotion, appraisal, and psychological construction. The basic emotion approach has been a major focus of studies in 'affective science', as studies of emotion have come to be called. The goal of researchers in this area is to discover and characterize the 'basic emotions', which are considered to be inherent in our biological endowment. However, in spite of years of research, there is still no consensus about the identity of the basic emotions. Tracy & Randles (2011) recently reviewed four models of basic emotions proposed by four prominent researchers in the area (Ekman, Izard, Levenson, Panksepp). Their lists of basic emotions are somewhat similar (fear is included in all four lists, and sadness, anger, and disgust are included in three of the four lists), but there are still many differences and many problems of definition of terms remain. Panksepp's (2005) list is the most divergent from the other three, which probably reflects the fact that he bases his list on his analysis of "the neurodynamics of brain systems that generate instinctual emotional behaviours" in various mammalian species, whereas the others base their lists on experimental studies of human subjects.

The appraisal approach assumes "that emotions are not merely triggered by objects in a reflexive or habitual way, but arise from a meaningful interpretation of an object by an individual" (p. 317). It considers the identification of emotional quality (its meaning) to require appraisal of the object and situation; it is the meaning that then leads to internal state changes: we are afraid of the bear when we see it (we appraise the situation) and then we become aroused and flee. Although Schachter & Singer use the word 'appraisal' in their theory, Gendron & Barrett consider their theory closer in content to the psychological construction approach.

The psychological construction approach posits that emotions are constructed out of more basic psychological ingredients that are not themselves specific to emotion. Two such basic components were proposed by Russell (2003): 'core affect' and 'affective quality'. "Core affect is that neurophysiological state consciously accessible as the simplest raw (nonreflective) feelings evident in moods and emotions" (p. 148). It is a single integral blend of two dimensions: pleasure-displeasure (which can range from elation to agony) and activation-deactivation (which can range from frenetic excitement to sleep). The feeling is an assessment of one's current condition. Affective quality is a property of the stimulus: its capacity to change core affect. Perception of affective quality together with core affect allows a person to construct the emotion. Barrett (2013) believes that psychological construction constitutes a paradigm for the scientific study of emotion that is different from the 'faculty' psychology paradigm of the basic emotion and appraisal approaches.

In another recent development, LeDoux (2012) has proposed rethinking the emotional brain in terms of survival circuits. The survival circuits proposed by LeDoux correspond almost exactly to behaviour systems as I have defined them, although he places more constraints on which brain circuits would be considered survival circuits. LeDoux also notes that his list of survival circuits does not align well with human basic emotions.

In considering these various approaches to the study of emotion, I have proposed that it is the activated behaviour system that determines the quality of the emotion (Hogan, 2017). The study of emotion then becomes the study of what behaviour systems exist in any organism, what motivational factors activate them, and how they are expressed. *Emotions are the subjective aspect of strongly activated behaviour systems*. A corollary of this conceptualization is that the felt emotion becomes an epiphenomenon: like the whistle of the steam engine, it has no causal significance—which is, of course, consonant with James's viewpoint. Much of the research on emotion in the past 50 years can be understood in these terms.

Non-human emotion

I have defined emotion as the subjective aspect (feeling) of strongly activated behaviour systems. Since we have no access to the subjective experience of any animal (except ourselves), any discussion of non-human emotion must rely on investigation of the expression of such strongly activated behaviour systems. One of the first systematic studies of the expression of the emotions in man and (other) animals was that of Darwin (1872). Darwin was primarily interested in similarities between animal expression of presumed emotional states such as anger, terror, and joy and human expression of these and other emotions. Darwin assumed that animals such as dogs, cats, horses, and monkeys had such emotional states, and tried to show that the expression of these emotions in humans could be traced to their expression in various animals as support for his theory of evolution.

Since we know that the nervous systems of all animals have similar components, it should be possible to infer the emotional state of an animal from observations of its behaviour. We would be inferring the state of activation of an animal's various behaviour systems, irrespective of whatever subjective experience the animal might be having. In effect, we would be performing a motivation analysis (see above). We have already seen examples of this with respect to the zigzag dance in sticklebacks and waltzing in junglefowl. A similar example is Lorenz's (1966) analysis of the facial expressions of fear and aggression in dogs (Figure 6.3). In this figure, increasing aggression goes from left to right and increasing fear goes from top to bottom. In (a) the dog is calm and unemotional; in (b) and (c) it is becoming more afraid; in (d) and (g) it is becoming more aggressive. The other figures depict ambivalent expressions. It can be seen that as fear is increasing, the ears and the corners of the mouth are drawn backward and downward; as aggression is increasing, the upper lip is raised and the mouth opened. This example shows that it is possible to ascertain which behaviour systems in an animal are activated. But how strongly does the system have to be activated in order to be considered an emotion? And how do we measure strength?

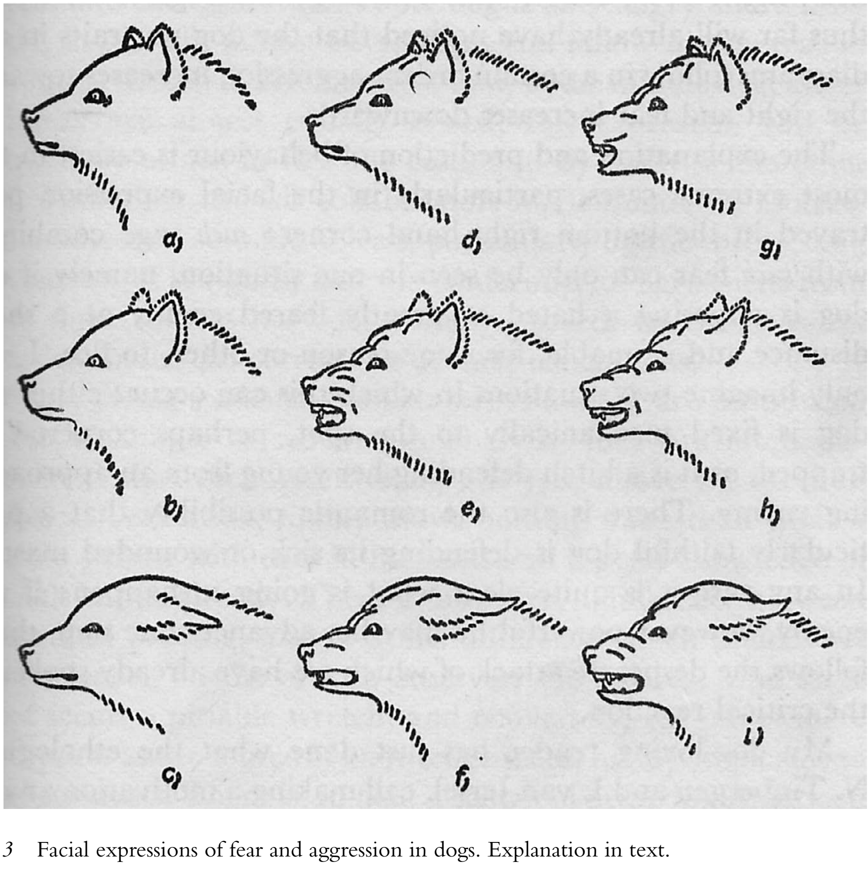

Figure 6.3 Facial expressions of fear and aggression in dogs. Explanation in text.

(From Lorenz 1966)

Strength has been measured both behaviourally and physiologically, and recently, ‘cognitively’ as well. An early investigator of ‘emotionality’ in animals (the rat in this case) was Hall (1934). He showed that defecation and urination in a standard situation were valid measures of individual differences in emotionality. Hall considered emotionality a trait, characteristic of an individual. He felt that attempts to differentiate specific emotions were extremely speculative. Hall, as also most prior and subsequent investigators of animal emotion, was really interested in using animal studies as a model for understanding human emotion. And soon thereafter, many other measures of bodily changes in animals, both behavioural and physiological, began to be used in investigations of various aspects of emotion. Paul et al. (2005) review the various approaches to measuring emotional processes in animals, past and present, including new non-linguistic cognitive measures.

Most studies of animal emotion are directed to understanding human emotion, but the rise of interest in animal welfare has led many investigators to study animal emotion *per se*. In the context of welfare, it is crucial to discover what makes an animal ‘feel good’ (or, at least, not suffer). Marian Dawkins (2008) suggests that a scientific study of animal suffering and welfare can be based on answers to two questions: Will the situation improve animal health? And, will it give animals something they want? The answer to the second question can be determined by discovering what the animal finds positively and negatively reinforcing (what they want and do not want) in a learning situation. Even here, however, a difference between ‘wanting’ and ‘liking’ (Berridge, 2004) makes interpretation of the results not straightforward (an animal may like something, but not want it at this moment). Nonetheless, Dawkins’s approach seems the most reasonable proposal to date. Theoretically, Mendl et al. (2010) have proposed a framework that integrates the *discrete emotion approach* (i.e., the basic emotion approach above) with the *dimensional approach* (i.e., the psychological construction approach above) for the study of animal emotion and mood. The cognitive aspects of the dimensional approach allow one to experimentally dissociate ‘liking’ something from currently ‘wanting’ it, which solves some problems. In all cases, however, the feelings of the animal remain a conjecture.

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7

COMPARATIVE COGNITION

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1. Historical Background

Comparative cognition investigates how information is represented, organized, and processed in different animals with the goal of understanding the function, phylogeny, ontogeny, and mechanisms of mental activity. Interest in this topic can be traced back, at least, to Aristotle (c. 384–322 B.C.E.) who compared behavioural tendencies and intellectual characteristics of different species (Leroi 2014). As with physical attributes, psychological traits that distinguished species, particularly those separating humans from animals, were considered immutable, a belief that permeated Western thinking for centuries. The idea that an entire species may change or adapt over time was put forward by Muslim scholars in the middle ages (Malik et al. 2017). This included Al-Jahiz (776–868), a zoologist in Iraq, who classified animals based on physiology and behaviour, proposing that environmental conditions drove adaptations that were advantageous for survival (Bayrakdar 1983). Darwin's theory of natural selection (1859) introduced these ideas to a Western audience, although the extent to which he and his contemporaries were influenced by the earlier Muslim writings is unclear (Guessoum 2011).

Darwin did not use the term cognition, but his proposal that mental faculties, such as memory, language, and emotion, were similar across species (Darwin 1871) laid the foundation for the later emergence of comparative cognition. His ideas challenged the Cartesian perspective, prevalent in Europe at the time, that only humans displayed complex thought, such as reasoning, or understood abstract concepts, such as time (King et al. 2016). Darwin's rejection of human uniqueness in intellectual abilities was consistent with ideas that were prevalent in some non-Western cultures (Malik et al. 2017). As an example, indigenous peoples of the Americas often attributed human-like psychological traits and cognitive abilities to other animals, noting that each species possessed specific knowledge and skills that allowed them to function effectively in their environment (Pierotti 2015). Humans, being the most recent species to inhabit the earth, were tasked with learning these skills from their animal cohabitants in order to survive in the same environments (Bruchac 1992). Regardless of whether he encountered these non-Western belief systems, Darwin made a unique contribution to the field of comparative cognition by articulating a process (i.e., natural selection) that explained the connection between environmental constraints and species-specific abilities. Even Alfred Russell Wallace, often considered a co-founder of Darwin's evolutionary theory, did not believe that psychological traits were shaped by the same forces that govern physiological adaptations (Wallace 1869).

By the late 19th century, proponents of Darwin's continuity theory undertook a series of studies purporting to demonstrate animal-human continuity in mental faculties: differences in degree, not kind. One of the most prominent, George Romanes (1892), collected circumstantial reports, often

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vivid and anthropomorphic descriptions of behaviour, as evidence for animal prowess in problem solving, empathy, and reasoning. Critics easily identified flaws in these anecdotal observations, noting that the existing experimental evidence provided no support for insight, intelligence, or other complex thought in nonhuman animals (Morgan 1894; Thorndike 1911). These advocates of the rising school of Behaviourism promoted an experimental analysis of behaviour using quantifiable measures of both stimuli and responses (Watson 1913), a perspective that dominated North American psychology in the first half of the 20th century.

Discussions of mental processes, as mediators of behavioural change, were minimized during the height of behavioirism, although not completely absent (Maier and Schnierla 1935). Tolman (1932) is often recognized for his foresight in suggesting that mental representations control responding in laboratory rats, and Kohler (1925) proposed that insight, not stimulus-response (S-R) learning, explained problem solving in chimpanzees. Less well known is the contribution of Charles Henry Turner (1867–1923), a biologist of African-American heritage, who openly challenged associative theories of the time by discussing mentalistic concepts in animals (e.g., intentionality, awareness, consciousness) while conducting controlled experiments with quantifiable measures (Abramson 2003; Lee 2020). Close to the same time, Margaret Floy Washburn (1871–1939) argued for a rigorous methodology in behavioural experiments, but advocated a more balanced approach in discussing the findings from these studies (Burghardt 2020). Over several editions of her text, *The Animal Mind* (first published in 1908)*,* Washburn rejected a strict behaviourist focus on stimulus-response learning, discussing higher mental processes, including consciousness, in a variety of species (Washburn 2010). Thus, North American Psychologists in the early 20th century generally agreed that animal behaviour should be measured in controlled, laboratory experiments, but disagreed on whether the outcome of these experiments could be explained without reference to non-observable thought processes.

Complementing these lab-based studies, research examining species-typical behaviours in the natural environment was advancing in central Europe. Specifically, champions of the emerging field of ethology (Lorenz, Tinbergen, and von Frisch) systematically examined causal determinants of responses that were part of an organism's behavioural repertoire (Dugatkin 2014). Like their behaviourist counterparts, ethologists devoted little time to discussing mentalistic concepts, although Lorenz (1950) proposed that fixed action patterns were initiated by central mechanisms ('action-specific energy'), and Tinbergen (1951) postulated that motivational impulses were generated in a central nervous system 'top centre'. In other words, a recognition that behaviour is controlled, or at least modified, by internal processes was overshadowed by a focus on detailed descriptions of observable phenomena, such as sign stimuli or fixed action patterns (Beer 2020).

Within the next decade, ethologists turned their attention to functional explanations, describing behaviour in terms of survival and reproductive advantage. From this, a subdiscipline of behavioural ecology arose, centered on topics such as inclusive fitness, kin selection, and foraging. Primary to the endeavour was the development of mathematical models of optimality: cost-benefit analyses of behaviour that maximized the reproductive and survival advantage of an organism (Dugatkin 2014). Although there was no expectation that individual animals consciously perform specific calculations to reach the best (i.e., most adaptive) solution in a given situation, the assumption was that natural selection had shaped biological mechanisms supporting computational processes of optimality.

As the influence of behavioural ecology spread, psychologists began to acknowledge that animal behaviour must be studied within the context of a species' evolutionary history. The point was epitomized in an experiment showing that rats easily associate a specific taste with nausea or a light-sound cue with shock, but failed to learn the alternate relationships (i.e., taste paired with shock or light-sound paired with nausea) (Garcia and Koelling 1966). This demonstration of differential sensitivity to specific cue-outcome associations fundamentally changed 'how we think about animal learning and its relationship to the rest of biology' (Shettleworth 2010b, pg. R910). Initial descriptions of this phenomenon as a 'constraint on learning' (Shettleworth 1972) emphasized the challenge it posed to behaviourist theories, specifically the idea that principles of stimulus-response learning could be generalized across stimuli and organisms. Evidence that evolutionary history determines the ease at which a species will acquire a particular association mounted rapidly, with 'selective associations' becoming the more commonly employed term (Shapiro et al. 1980). Eventually, many researchers adopted the term 'adaptive specializations' (Shettleworth 2010a), highlighting the belief that behaviour is tied to a biological system that evolved to meet the functional needs of a particular species (Hulse 2006).

2. A Focus on Cognition

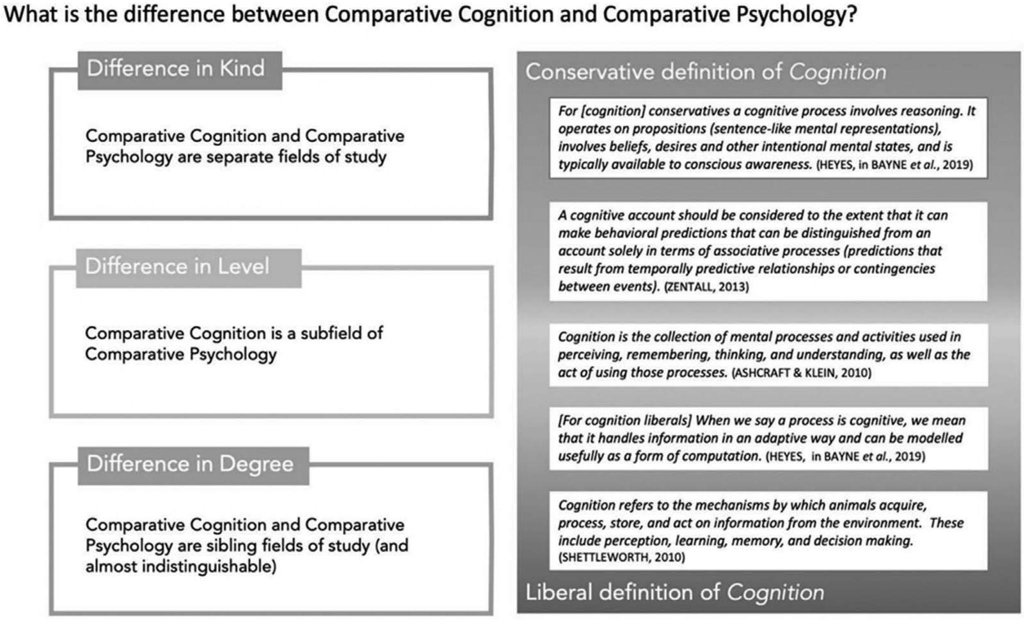
The idea that evolutionary factors shape psychological processes, at least in humans, was exemplified in Chomsky's theory of universal grammar (Chomsky 1968). His scathing rejection of a behaviourist explanation of language acquisition (Chomsky 1959) coincided with Simon and Newell's infamous proposal (1959) that mental activity is analogous to computational processing in computers (Lachmann et al. 1979). Theories and methodologies from both linguistics and computer science soon infiltrated other fields, most notably psychology, with terms such as storage, retrieval, and symbolic representation entering the lexicon of this discipline (Ashcraft and Klein 2010). Animal researchers soon adopted a similar perspective, using principles of information processing to explain complex abilities such as spatial navigation, decision making, and tool use in nonhumans (Shettleworth 2010a).

By the early 1980s, cognitive psychology was firmly established as one of the dominant trends in academic research. Cognition, defined more than 500 years ago as the action or faculty of knowing (Chaney 2013), became an umbrella term for a collection of mental processes ranging from perception to language. The notion that cognition included all processes by which sensory input is transformed, reduced, elaborated, stored, recovered, and used (Neisser 1967) implied that cognitive research included anything *not* studied by behaviourists. More explicitly, cognition was assumed to involve emergent, untrained responses rather than learned S-R associations (Wasserman and Zentall 2006). The distinction was particularly apparent in discussions of learning and memory, the former studied in animals by behavioural psychologists, and the latter in humans by cognitive psychologists.[1] Over time, this 'old and misplaced' dichotomy (Emery 2017) was difficult to justify in that 'reflex and reinforcement-based explanations suggest one type of representation, not alternatives to the concept of representation' (Roitblatt 1987, page 19).

There are three categories of opinion regarding the difference between comparative cognition and comparative psychology.

1. Difference in kind. Comparative cognition and comparative psychology share some features but are fundamentally distinct fields (e.g., Abramson 2015).
2. Difference in level. Comparative cognition is a subfield of comparative psychology. This view is exemplified by textbooks such as Greenberg and Haraway's *Principles of Comparative Psychology* (2002), in which animal cognition is covered in a separate chapter. This *Handbook of Comparative Psychology* adopts the same perspective.
3. Difference in degree. Comparative cognition and comparative psychology are sister fields; to carry the metaphor further, cognitive ecology (Chapter 8) is the monozygotic twin of comparative cognition. For some, comparative cognition and comparative psychology are so closely related as to be almost indistinguishable, with the terms sometimes being used interchangeably (e.g., McMillan and Sturdy 2015; Shettleworth 2010a).

Which of these three opinions one holds is related to how one defines *cognition*, which can range from more conservative to more liberal (Heyes, in Bayne et al. 2019). Liberal definitions are broad enough to include such phenomena as perception, memory, categorization, and associative learning,



What is the difference between Comparative Cognition and Comparative Psychology?

Difference in Kind

Comparative Cognition and Comparative Psychology are separate fields of study

Difference in Level

Comparative Cognition is a subfield of Comparative Psychology

Difference in Degree

Comparative Cognition and Comparative Psychology are sibling fields of study (and almost indistinguishable)

Conservative definition of *Cognition*

For [cognition] conservatives a cognitive process involves reasoning. It operates on propositions (sentence-like mental representations), involves beliefs, desires and other intentional mental states, and is typically available to conscious awareness. (HEYES, in BAYNE *et al.*, 2019)

A cognitive account should be considered to the extent that it can make behavioral predictions that can be distinguished from an account solely in terms of associative processes (predictions that result from temporally predictive relationships or contingencies between events). (ZENTALL, 2013)

Cognition is the collection of mental processes and activities used in perceiving, remembering, thinking, and understanding, as well as the act of using those processes. (ASHCRAFT & KLEIN, 2010)

[For cognition liberals] When we say a process is cognitive, we mean that it handles information in an adaptive way and can be modelled usefully as a form of computation. (HEYES, in BAYNE *et al.*, 2019)

Cognition refers to the mechanisms by which animals acquire, process, store, and act on information from the environment. These include perception, learning, memory, and decision making. (SHETTLEWORTH, 2010)

Liberal definition of *Cognition*

Figure 7.1 The relationship between definitions of cognition and how these relate to comparative psychology versus comparative cognition.

as well as the formation of representations that allow for flexible problem solving across contexts. More conservative definitions of *cognition* exclude processes such as associative learning, instead emphasizing reasoning and inference.

Although cognitive psychologists continue to debate which processes are to be included in their field of study, there is general agreement that cognition involves the representation, organization, and processing of mental information. This occurs through computational mechanisms linking sensory input to behavioural output. Hebb (1949) formulated one of the earliest accounts of this process, proposing physiological underpinnings of mental activities, such as memory. Technological advances over the subsequent 70 years dramatically enhanced the ability to investigate biological structures and function, leading to a consensus that cognition is an emergent property of brain activity (Wasserman and Zentall 2006). A natural outcome of this idea was the recognition that cognition is a set of adaptive traits, which evolved to solve fitness-related problems (Shettleworth 2010a).

In this chapter, we adopt a multi-faceted view of cognition that encompasses mental activities supporting attention, learning, memory, concept formation, decision making, reasoning, and communication, among others. Researchers may disagree with the specific categories of cognitive processes (as well as how these are organized), but there is growing consensus that processes can be characterized by distinct rules of operation. Domain-general processes, such as perception, attention, and memory, are ubiquitous across many species; they are also building blocks of domain-specific processes (Shettleworth 2010a). At a conceptual level, domain-specific processes can be divided, further, into two categories: those that allow a species to interact adaptively with the physical environment (e.g., navigation, timing, and physical causality) and those that allow a species to interact adaptively with the social environment (e.g., social competence, prosocial behaviour, and communication). A primary challenge in the field is to understand the relationship between these different processes, as well as how they interact with other systems and functions (e.g., motivation, temperament, and motor patterns) to produce flexible and adaptive behaviour (Burghardt 2019).

Finally, the contemporary field of comparative cognition is built on three assumptions. The first is that cognition can be studied scientifically in humans and other animals. Early work in this area included a series of studies assessing the ability of phylogenetically distant species animals to solve the same series of tasks, often with mixed conclusions (Bitterman 1975). A recognition that comparisons were compromised when animals possessed dramatically different sensory and motor capabilities helped to move the field from a focus on general intelligence to an examination of cognitive processes adapted to unique ecological niches of each species (Pearce 2008). The second assumption is that cognition, as a byproduct of biological functioning, is subject to the laws of natural selection. This explains the principle of proper mass (Jerison 1973) in which the proportion of brain area devoted to a cognitive function reflects the relative importance of that function in terms of evolutionary advantage. Evidence supporting this claim includes dramatic differences in the size of visual processing areas of diurnal and nocturnal rodents (Striedter 2005), and in hippocampal volumes of closely related bird species that experience varied environmental demands on food caching (Balda and Kamil 2006). A further corollary is that there must be heritable, within-species variability in the cognitive traits that provide an adaptive advantage (Boogert et al. 2018). Investigations in this area have not, traditionally, been a mainstay of comparative cognition research, partly because of the difficulty in assessing variability in cognitive processes (Morand-Ferron et al. 2016), although the trend is slowing changing (Griffin et al. 2015). The third assumption of comparative cognition research is that scientific questions will be addressed using two or more species. If a particular research study involves only one species, the findings will be compared to other studies using different species. A critical point, not always appreciated by those outside of the field, is that cross-species comparisons need not include *Homo sapiens*. Indeed, anthropomorphism promotes the incorrect and misleading assumption that humans are at the apex of a phylogenetic scale (Shettleworth 2010a).

3. Comparative Studies of Cognitive Structure

3.1 Architecture of Cognition

As in the broader the field of cognitive science, comparative cognition researchers continue to debate the architecture of cognition. Discussions of this topic have moved from evaluating the merits of general processing (MacPhail 1987) versus adaptive specialization (Gallistel 1998) views of cognition, to describing the relationship between domain-general and domain-specific processes (see Burkart et al. 2017 and commentary). Despite ongoing work, a number of issues are unresolved, partly because the criteria used to distinguish domain categories remains controversial. Specifically, domains are defined by functional outcomes (e.g., locating cached food items) but the operations and mechanisms that support those outcomes may be parsed in multiple ways (e.g., integration of landmark cues, reference memory, timing, etc.). In other words, there is not a one-to-one mapping from cognitive process to adaptive outcome, making it difficult to ascertain a direct relationship between the two.

Adding further complication, the term 'domain-general' is used in at least two different ways by comparative researchers. Shettleworth (2010a) uses it to describe basic cognitive processes with the following properties: information is processed in a relatively stereotypical manner, regardless of the specific input; each process can serve multiple functions, which may occur simultaneously; and principles of operation are preserved across species. In this schematic, domain-general processes are the foundation of domain-specific processes, which are preferentially attuned to the functional demands of an organism. As an example, the domain-specific process of inter-species communication depends on the domain-general process of perception (among others). In a different formulation (Burkhart et al. 2017), domain-general describes a higher-order process that emerges from an interaction between multiple cognitive specializations. According to this view, domain-general thinking (often equated with general intelligence) describes the mental operations that integrate domain-specific processes. Originally formulated as a human-unique trait, it is now clear that many other animals share this cognitive ability, although the extent to which it is represented across phylogeny is still unclear (Laland and Seed 2021; Poirier et al. 2020). Importantly, the capacity for domain-general thinking does not preclude the existence of cognitive specializations; humans and many animals are capable of combining functionally distinct cognitive processes in flexible ways, allowing them to respond adaptively to changing environmental demands.

In sum, the relationship between domain-general and domain-specific processes is often represented in one of two ways. In the first, domain-general processing is a foundation for domain-specific processing. In the second, domain-general thinking emerges from domain-specific specializations. A more viable hypothesis is one in which the two frameworks are overlaid such that basic, ubiquitous operations support specialized functions, which are then integrated across domains to yield flexible and adaptive responding (Burkart et al. 2017).

3.2 A Working Model

While recognizing that disagreements on the nature of mentality (i.e., cognitive structure) are unlikely to be resolved in the near future, a model in which specialized abilities build on basic and ubiquitous operations (Shettleworth 2010a) provides a useful heuristic for studying cognition in different animals. For example, if domain-general processes are comparable across species, it should be possible to examine the operations and functions of domain-general processes using a similar set of protocols. This approach has been applied to attention, which is present in species ranging from honeybees to humans, facilitating and supporting adaptive behaviours, such as foraging and mate selection. Comparative studies of the limitations and capacities of attention helped to uncover its plausible structure, leading to the proposal that this multidimensional construct includes at least three separable factors: focusing, scanning, and sustaining attention (Washburn and Taglialetela 2006). It should go without saying that subsequent modifications to this theory must account for research findings from studies using a range of species.

In a separate line of work, comparative studies of domain-specific processes have helped to refine contemporary ideas of cognitive structure. This work often focuses on identifying links between specialized cognitive abilities and distinct environmental demands facing a species. A classic example is superior memory, specifically for spatial locations, in corvid species that rely on food caching to survive harsher winters (Balda and Kamil 1989), supporting the idea that the refinement of domain-specific processing is an adaptation to environmental constraints of a species. The parameters of a memory system that support this behaviour are likely to be functionally incompatible with those that support song learning in birds (Sherry and Schacter 1987). The idea that memory for different types of information may have distinct principles of operation helped to solidify the concept of multiple memory systems, that developed from clinical and preclinical lab studies (Squire and Zola-Morgan 1988).

The role of comparative work in advancing our understanding of domain-specific processing can be extended to other research topics. For example, the idea that separate memory systems are characterized by different properties, constraints, and biological mechanisms was consistent with a modular theory of cognitive structure (Fodor 1983), and with the proposal that adaptations serving one function cannot effectively serve another (Cosmides and Tooby 1994). Further comparative work, however, challenged these models, revealing instead that distinct operations in separate domains need not be functionally incompatible (Jacobs and Gardenfors 2017). Similarly, although anatomical localization of functional systems is consistent with the principles of a multiple memory system model, it is not a prerequisite for domain-specific processing (Glascher et al. 2010). In other words, an organized cognitive structure can be produced by coordinated integration of brain activity across multiple anatomical regions (Duncan et al. 2020). The phenomenon is not limited to humans in that nonhuman primates show similar patterns of activation across multiple neural sites in response to specific cognitive demands. Comparative work that incorporates contemporary neuroscience approaches can reveal the extent to which this phenomenon extends across phylogeny, possibly revealing new principles of cognitive organization and its evolution.

3.3 Domain-specific Interactions

As described in Section 2, domain-specific cognitive processes can be divided into at least two categories: those that allow a species to interact adaptively with the physical environment and those that allow a species to interact adaptively with the social environment. The first category includes cognitive processes such as spatial navigation, counting, and an understanding of physical causality whereas the second includes communication, theory of mind, and social learning, among others. As with domain-general categories, domain-specific processes are not functionally distinct: adaptive behaviours are supported by interactions within each of these categories. In terms of physical cognition, seasonal migration of many bird species relies on both spatial navigation and timing (i.e., circadian cues) (Wiltschko and Wiltschko 2003). Similarly, within the social domain, a combination of social competence (i.e., an understanding of group hierarchies) and conspecific communication facilitates reproductive success in vervet monkeys (Seyfarth and Cheney 2003).

Additionally, cognitive processes may interact across physical and social domains to produce complex behaviours, such as tool use. Flexible tool use that includes the manufacture, modification, and sequential use of tools is rare yet phylogenetically spread, with well-studied examples from birds (e.g., New Caledonian crows) and nonhuman primates (e.g., chimpanzees and capuchin monkeys). Comparative work suggests that flexible tool behaviours require domain-general processes such as inhibition of prepotent responses, but also specialized attention to relevant physical features of objects (for review, see Visalberghi et al. 2017). Crows, chimps, and capuchins, for example, show some sensitivity to the causal features of tools (e.g., shape, connectivity, rigidity) in learning the association between the tool movement and its outcome (Hoffman et al. 2016). The development of tool use occurs in a social context, though, and is supported by social learning mechanisms: novice tool users observe the behaviour – or outcomes of the behaviour – of local experts. It is thus proposed that complex tool use may only be seen in species with extended parental care or a certain degree of social tolerance which, in turn, creates social learning opportunities (van Schaik et al. 1999). Indeed, species with the greatest contextual diversity of tool use are those with increased reliance on social learning (Visalberghi et al. 2017).

4. Challenges and Next Steps

4.1 Assessing Cognition

The primary challenge in comparative cognition research was articulated more than 100 years ago: "knowledge of the animal mind, like knowledge of human minds … must come by way of inference from behaviour" (Washburn 1908, page 4). Washburn goes on to note that a first step in this endeavour is the identification of behavioural tests that provide operational definitions of mental activity. The task has become increasingly complex over the last century as evidence accumulates that cognition is a multi-faceted construct. Researchers in this field have long advocated employing multiple tests of the same function (Beran et al. 2014; Bitterman 1975; Macphail 1987; Roitblatt 1987; Shettleworth 2009, 2010a), a triangulation approach that acknowledges the need to examine complex processes (i.e., cognition) from multiple perspectives (Heyes 1993). A goal of this approach is to identify a common set of tasks that tap into specific constructs of cognition (e.g., working memory), which are then linked to underlying biological mechanism. Dividing cognitive constructs into smaller components (e.g., working memory can be parsed into active maintenance, flexible updating, and limited capacity) makes it easier to identify those that are shared among species, under what conditions, and why (Shettleworth, 2009). In addition, grouping individual components based on commonalities in mechanism or function may uncover relationships among cognitive processes in animals that were not otherwise apparent: a 'forest rather than trees' approach that encourages cross-talk among researchers studying different phenomenon (Beran et al. 2014).

Most importantly, the recognition that behavioural measures of cognition in nonhumans must be sensitive to the context in which the behaviour occurs increased the use of ecologically valid paradigms and reduced the tendency for anthropomorphic interpretations of animal behaviour (Shettleworth 2009). At the same time, research that relied on naturalistic behaviours revealed some surprising abilities in nonhumans, including evidence for cognitive faculties such as tool use, numerical competence, and social learning in insects (Chittka et al. 2019). The extent to which these processes are analogous to those in other species has yet to be determined. Finally, any behavioural measure of cognition must yield a range of scores across a population in that the adaptive value of a cognitive process cannot be assessed in the absence of individual variability in these traits (Boogert et al. 2018).

4.2 Diversity of Species Studied

Comparative cognition, like its parent discipline of comparative psychology, consistently faces the question of whether the field is truly comparative (Beran et al. 2014). In the early 20th century, Washburn (1908) summarized contemporary research on animal thought in more than four dozen species, ranging from amoebas to crayfish to cows. By the middle of the century, the number of species represented in comparative psychology publications had declined dramatically, with an increasing number of studies using a single species, most commonly the rat (Bitterman 1960). This tendency is generally attributed to the dominance of behaviourism in psychology, and the ensuing belief that principles of learning were ubiquitous across species. The trend was reversing by the late 1990s, particularly as comparative cognition became an independent field and incorporated methodologies and perspectives from ethology into the discipline (Shettleworth 2009). If the current volume is an accurate reflection, comparative psychology, itself, is broadening the range of species it studies, with different chapters covering research on a variety of invertebrate, reptilian, fish, avian, and mammalian species.

The challenge now facing comparative researchers is that access to many species is declining. Tragically, we know very little about the natural ecology and behaviour of some endangered species (e.g., pangolins), making it difficult to develop policies and practices to ensure their survival (DiPaola et al. 2020). Research in animal cognition can make a valuable contribution to conservation practices by identifying cues, mechanisms, or experiences that could improve the efficacy of behaviourally oriented manipulations (Greggor et al. 2014). As an example, collisions with manmade structures, which are directly linked to population declines of many avian species, could be reduced by practices that incorporate knowledge of attentional biases, social learning, or other cognitive processes displayed by these animals (Martin 2011). In addition, associative learning, specifically taste aversion training, is an effective means to reduce ingestion of cane toads (which are both invasive and toxic) by native Australian northern quolls (O'Donnell 2011); a similar methodology may be a non-lethal means to reduce nest predation by pied crows in South Africa (Ferguson et al. 2021). These cognitive-based approaches are particularly attractive as conservation tools in that they are generally less expensive and easier to implement than traditional methods of animal control (e.g., culling, trapping, translocation, or poisoning), that often introduce ethical concerns of their own.

A separate line of work builds on comparative cognition research to increase the well-being of animals in zoos, helping to improve reproductive success of endangered animals in captivity (MacDonald and Ritvo 2016). Some of these principles are being incorporated into external settings, such as ecotourism, in which high levels of stress may interfere with breeding and other naturalistic behaviours (Pichegru et al. 2016). This work will become increasingly important in the future as the rate and impact of human–animal interactions is likely to increase.

4.3 Ontogeny

Comparative cognition researchers frequently refer to Tinbergen's four questions of behaviour as guiding principles in their field, noting that a comprehensive understanding of any cognitive process requires knowledge of function, phylogeny, ontogeny, and mechanisms. Of these four, there are relatively few theories of cognitive development in animals, particularly compared to human research (Sabbagh 2020). Notable exceptions include communication in songbirds (Searcy and Nowicki 2019) and the mapping of developmental milestones in chimpanzees (Brundl et al. 2021). Admittedly, the task is not straightforward, particularly when research on animal cognition is conducted in the natural environment. One of the biggest challenges in this work is disentangling ontogeny from phylogeny, particularly as environmental experience can dramatically alter biological systems that support cognition. For example, a larger hippocampal volume in food storing birds could reflect an adaptation to ecological constraints of food shortage, increased experience with caching and recovering food, or a combination of the two (Shettleworth 2012).

Despite these difficulties, comparative cognition research would be enriched by a wider discussion of developmental processes in nonhumans, specifically how cognition emerges and adapts over a lifetime. As an example, individual differences in cognitive abilities are often exacerbated as humans age, but it is not clear whether this is a general principle of neurobiological development or a byproduct of human society and culture. In addition, the performance of very young children on many cognitive tasks (e.g., theory of mind, numerosity, physical causality) is often closer to that of animals than to human adults (Shettleworth 2012), but how these processes emerge in young animals is largely unknown. Importantly, comparative studies of cognitive development should not be limited to early life in that changes in cognition are likely to occur across the lifespan in species other than humans. The time may be ripe to undertake this work as recent technological advances in molecular biology (i.e., epigenetic) provide exciting new opportunities to understand the relationship between maturational and experiential factors in shaping cognition.

5. Conclusion

A primary goal of comparative cognition research is to further our understanding of cognitive evolution (Roitblatt 1987). As outlined in this chapter, the work may also provide insight into principles that govern these two independent subjects (i.e., cognition and evolution). Indeed, more than half a century beyond the establishment of cognitive science as an independent discipline, unified theories of mental structure, as well as descriptions of operations that may instantiate such theories, are lacking (Laird et al. 2017). Comparative studies could inform these discussions, potentially leading to novel conceptualizations of how general and specialized cognitive processes may be linked, both functionally and mechanistically (Burkart et al. 2017). In terms of understanding evolution, the use of sophisticated molecular biology tools combined with large-scale data collection across a variety of species has allowed researchers to reconstruct phylogenetic maps of animal cognition (Emery 2017). A complementary line of work employing ecologically valid paradigms revealed how similar cognitive processes emerged in distantly related species, reinforcing the tenet that evolution is not restricted to homology (Emery and Clayton 2004). Finally, the primary message of all comparative work, cognition or otherwise, is that diversity is critical for survival, both within and across species.

Note

1. As we frequently ask our students, how could learning be present without memory (and vice versa)? And if it were, how would it be measured?

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Queen's University is situated on traditional Anishinaabe and Haudenosaunee Territory.

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8

COGNITIVE ECOLOGY

Julie Morand-Ferron

A Brief History

If you ask one hundred people what they think of when you refer to the phrase "animal cognition", those who have heard the term will probably refer to examples of animal intelligence seen in documentaries, such as chimpanzees using sign language, corvids filling a pitcher of water with rocks to obtain food floating on top, or rats pressing a lever in a skinner box. Very few will refer to the role of learning and memory in functional behaviour occurring in the wild, or to how cognitive traits are molded by the environment, and how this shapes their evolution. This is the domain of *"cognitive ecology",* which integrates knowledge on proximal causes of behaviour (cognitive, neurobiological) with ultimate explanations for the evolution and maintenance of variation in cognitive processes and abilities (Dukas 1998; Healy and Braithwaite 2000; Sherry 2006).

Cognitive ecology takes an evolutionary biology perspective on cognitive processes such as perception, learning, memory and decision-making and their associated neural structure(s). The suggestion that cognitive traits are the product of evolution is not a new one; it was already present in Darwin's writings and probably even before this time (cf. Chapter 6; Olmstead and Kuhlmeier 2021). In the early 20th century, ethologists examined the evolution of decision-making in the selective context of their study species (Tinbergen 1963; Hinde 1970). The discovery of adaptive specializations (Rozin and Kalat 1971) and the development of comparative psychology then continued to move this idea forward. Cognitive ecology is contributing additional avenues borrowed from evolutionary biology research to try and unravel cognitive evolution. These approaches include examining evolution occurring in controlled conditions (i.e. experimental evolution, artificial selection) and assessing the contribution of cognitive traits to survival and reproductive success in the wild (Morand-Ferron et al. 2016). The aim of cognitive ecology is to place cognition together with morphological, physiological, behavioural and life-history traits examined by evolutionary biologists (Dukas 1998). In contrast to the >100 years of research on animal psychology and on the evolution of non-cognitive traits, the evolution of cognition is a fairly unexplored topic, maybe because it requires an integrative approach, i.e. applying evolutionary theory to cognitive processes studied by psychologists. Hopefully, the co-existence of comparative cognition and cognitive ecology should help ensure further cross-fertilization between the disciplines, by bringing the attention of psychologists to evolution, and of evolutionary biologists to cognition.

In the paper where he coined the term "cognitive ecology", Real (1991) indicates that few behavioural ecologists recognized at the time that characterization of ecological parameters that went into the mathematical models of behaviours (e.g. densities, rates, spatial locations) relied on

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cognition, and thus that cognitive processes are central in explaining behaviour. For instance, the early empirical tests of models of prey choice in great tits (*Parus major*) led to the finding of "partial preferences" rather than an all-or-none preference for the most profitable prey type, as predicted by theoretical models (Krebs et al. 1977). This phenomenon can be explained by the adaptive value of updating information on alternative options in natural conditions, which are usually more variable than experimental set-ups. Optimality models then gained predictive power by incorporating parameters for information gathering and learning. Animal cognition researchers have since then worked to 'open the black box' of cognition (Giraldeau 2004), and figure out what animals perceive, pay attention to, learn and memorize in their environment (Ducatez et al. 2020; Lee and Thornton 2021).

The term "ecology" in cognitive ecology refers to the need to understand behaviour in the natural context in which it evolves. Classic studies in cognitive ecology originated from examining challenges that animals must overcome to find resources, such as food and mates. For instance, scatter-hoarding birds spending the winter in temperate climates cache food in multiple locations in their home range. Sherry (1984) demonstrated a role for spatial memory in remembering the location of these caches, by allowing black-capped chickadees (*Poecile atricapillus,* Figure 8.1) to cache and retrieve food in the lab. Comparative work then contrasted hoarding and non-hoarding bird species in terms of spatial memory performance and hippocampus size, a neural substrate shown to be important for the retrieval of spatial information (Krebs et al. 1989). Other classic studies include the covariation between mating system, spatial memory and hippocampus size in voles. In polygynous vole species, males have larger home ranges, higher spatial ability, and a larger hippocampus than females, while these sex differences are not found in monogamous vole species, where there is no reproductive advantage for males to remember and visit the location of multiple females (Gaulin and Fitzgerald 1989; Jacobs et al. 1990). The success of the comparative approach linking ecology, cognition, and the brain in a coherent adaptive story was to motivate a whole suite of studies on various topics and taxa (cf. Dukas 1998; Sherry 2006; Dukas and Ratcliffe 2009; Ratcliffe and Phelps 2019).

While early cognitive ecology studies already adopted an evolutionary approach when framing their hypotheses, they relied on the assumption that cognition evolves as a set of traits under natural

Figure 8.1 Black-capped chickadee eating a mealworm. Chickadees and their European relatives, such as the great tit, are commonly studied species in cognitive ecology.

Photo credit: Catherine Jarjour.

selection, without providing direct empirical tests of this assumption. Indeed, they mostly examined the adaptation process that occurred in the past by comparing species (macroevolution) and did not examine current selective pressures, such as whether individual variation in cognition is correlated with fitness in contemporary populations (microevolution, but see Spritzer et al. 2005). The adaptive value of information gathered through learning had however been demonstrated in a few elegant laboratory experiments conducted in the 1990s. For instance, blue gouramis (*Trichogaster trichopterus*) that were conditioned to associate a light to the appearance of a receptive female fish had a paternity advantage over control males that were presented with unpaired light and females. This paternity advantage occurred through the learned ability of experimental males to reduce their initially high levels of aggression and initiate courting behaviours upon encounters with potential mates (Hollis et al. 1997).

It will then take several years before researchers start using naturally occurring variation in cognitive phenotypes – instead of creating variation via an experiment, as described above – and analyse it against wild estimates of fitness, to directly assess selection in contemporary populations (Cole et al. 2012). This time lag might be due to the combined difficulties of measuring cognitive performance and reproductive success in a large sample of wild individuals, but also partly to the scarcity of studies using a similar approach on "labile" traits, such as behaviour. Indeed, evolutionary biologists have been measuring the strength of natural selection for several decades, but have mainly examined other types of traits: morphology, life-history, physiology, and only recently, behaviour (Kingsolver et al. 2001; Réale et al. 2007). Studies on the covariation between cognitive performance and fitness components are now blossoming, reporting cases where high cognitive performance is positively, neutrally, as well as negatively correlated with fitness components (reviewed in Boogert et al. 2018).

Below, I gathered examples of studies on these themes: (1) What is the role of asocial and social environments in generating cognitive variation? (2) What is the role of cognitive variation in determining survival and reproduction, and ultimately fitness? Please note that it would be out of the scope of this chapter to present a complete overview of each of these themes, and that other approaches could equally be brought together under the "cognitive ecology" umbrella (e.g. role of cognition in functional behaviour, which intersects with comparative cognition, cf. Chapter 6). The fact that I could have included many more exciting studies than those I was able to cover in this chapter seems in itself evidence that the field is "of substance" nowadays, as it was at the turn of the millennium (Healy and Braithwaite 2000).

Cognition & the Environment

Non-social Drivers

Researchers have used variation in the extent of ecological challenges to make predictions on the corresponding evolutionary impact on cognition. One of these environmentally driven hypotheses is the "harsh environment hypothesis". This hypothesis was initially formulated (Pravosudov and Clayton 2002) for scatter-hoarding birds that store food items in several locations and make use of spatial memory to retrieve these scattered caches during the winter. Researchers have co-opted ecological gradients (latitude, altitude) to test predictions across different populations of the same species living in contrasting environments, where harsher winter conditions at higher latitude and elevation are assumed to result in more intense selection pressures on hoarding behaviour, and thus on the accompanying spatial cognitive abilities. Black-capped chickadees living at higher latitude in North America, and thus experiencing longer and colder winters, demonstrated heightened food-hoarding tendencies in the laboratory, more accurate spatial memory and higher hippocampal neuron count than populations living in milder climates (reviewed in Pravosudov et al. 2015). These differences were also observed when comparing birds who had been brought to the lab as very young chicks that had not left the nest yet (i.e. common garden experiment; Roth et al. 2011), which reinforces the conclusion that the observed differences are the result of divergent natural selection rather than plasticity arising during development. Compared to birds taken from nests in Kansas, birds from Alaska were also found to have a larger telencephalon, a portion of the avian brain mediating general cognitive processes (e.g. learning, integration of information from various senses), and were faster at solving a new food-motivated problem, suggesting that harsh environments also select for other cognitive abilities not related to food-hoarding or spatial memory (Roth et al. 2010). This latter idea has been examined at the comparative level using a worldwide database on avian foraging innovations – new feeding behaviours not previously observed in a species – extracted from short communications in ornithology journals. As expected under the "harsh environment hypothesis", as well as the "cognitive buffer hypothesis"(Sol and Lefebvre 2008), innovations are more prevalent in species living at higher latitudes, and are also recorded more often in winter than in other seasons (Sol et al. 2005). These findings suggest that low food availability and physiologically demanding weather can promote innovative behaviour, which could itself select for improved learning ability and larger brain regions underlying general cognitive abilities (reviewed in Lefebvre et al. 2013).

In non-hoarding species, general cognitive abilities such as associative learning and/or an ability to reverse associations could contribute to tracking highly variable food sources in harsh environments (Morand-Ferron et al. 2019). For example, Tebbich and Teschke (2014) compared woodpecker finches (*Cactospiza pallida*) captured in a dry area where food availability is highly variable and dependent on occasional rainfall, with those from a cloud forest where food abundance is stable. They found no significant difference in problem-solving performance, but in support of the harsh environment hypothesis, reported birds from the more variable environment to outperform their conspecifics on a reversal learning task. Moreover, a study on parasitoid wasps reported higher associative learning performance for host cues in populations living in the wild, where prey density is much lower – and thus the environment is harsher – than in conspecifics living in buildings such as granaries, where prey are easier and cheaper to locate (Froissart et al. 2017). In contrast, a study on serial reversal learning in great tits from several sites at low and high elevation in the Pyrénées reported no elevation difference in the first reversal learning task, but higher accuracy over all reversals in birds from low elevation sites, where winter conditions are less severe (Hermer et al. 2018). This effect goes against predictions of the harsh environment hypothesis, and has several potential explanations (also discussed in Morand-Ferron et al. 2019). For instance, because birds were tested in small groups where each bird progressed at its own pace on the task, copying the choice of conspecifics on this two-option task would have resulted in an average 50% chance of being correct (at any moment, about half the birds were rewarded for pecking the left key, while the other half had to peck the right key of the operant device). If birds from high elevation tended to rely more heavily on social information, this could explain their lower performance; however a post-hoc analysis found no elevation difference in the likelihood that a bird copied the previous choice expressed by a conspecific (Hermer, unpubl. results). One likely explanation for the results in Hermer et al. (2018) is that other selective agents act on cognitive processes determining reversal learning performance. For instance, social group size or food diversity could be higher at low elevation sites and have a stronger impact on the capacity to quickly form and update associations, as well as inhibit previously learned behaviours. This difficulty at disentangling potential causal factors for population or species-level comparisons is one of the main issues with the comparative approach; ideally researchers should identify populations that are contrasted on the hypothesized factor, but do not differ for the main confounds, which is not easily done when these factors tend to covary.

An approach that allows direct examination of the effect of putative selective agents is experimental evolution. In these experiments, replicated populations evolve in the lab, in conditions that are identical as much as possible except for the factor of interest: temperature, population density, etc. It is then possible to assess whether the descending populations differ in the predicted direction for a given set of traits. This approach has been used with *Drosophila melanogaster* to test long-standing hypotheses on the effect of environmental parameters on the evolution of learning. Dunlap and

Stephens (2009) compared populations evolving in environments that either had informative or non-informative cues for laying substrate quality, in environments where the best action was either fixed or variable between generations. After 30 generations, naïve offspring from lines evolving in environments where experience was reliable and the best medium changed over each generation (such that an innate preference could not evolve) showed higher learning score when choosing a laying substrate. Together, these experiments (see also Kawecki 2010) highlight the potential for rapid evolution of learning ability, at least in organisms with short generation time.

Experimental translocation between environments can also be used to examine the effect of selective agents on the evolution of traits of interest, but because these experiments occur in the wild, co-varying factors may still be confounded with the factor of interest. Mitchell et al. (2020) translocated guppies (*Poecilia reticulata*), from a single high-predation site to four low-predation sites and measured relative brain size after eight to nine years of natural selection in the wild. Previous studies had shown an anti-predation advantage for large-brained females (Kotrschal et al. 2015); it is thus surprising that the translocated populations actually showed no change or an increase – rather than a decrease – in relative brain size after the relaxation of predation pressure. Possible explanations include an effect of unmeasured factors, such as a higher intensity of intra- and interspecific competition at low predation sites, the demands placed on brains by the need to adjust to new conditions following the translocation (cognitive buffer hypothesis; Sol 2009), natural selection acting on life-history and body size which is reflected in the relative brain size measurement, or noise in the relative brain size–cognition relationship (Smaers et al. 2021). To my knowledge, this type of ambitious experimental translocation and follow-up of local adaptation has not been applied to measurements of cognitive performance, an approach that could help resolve some of the questions raised by this pioneering experiment.

Social Drivers

While the above-mentioned studies have focused on the role of (mostly abiotic) environmental conditions as potential drivers of cognitive evolution, other studies have examined the social environment. Many aspects of social interactions have been postulated to impact the evolution of cognitive traits, including: contests and aggression (reviewed in Reichert and Quinn 2017), mate detection and selection (reviewed in Ryan et al. 2009), and mate displays (reviewed in Boogert et al. 2011). In particular, experimental evolution has been used to assess the role of sexual selection in the evolution of male cognitive traits. While *D. melanogaster* are usually polygynous, Hollis and Kawecki (2014) suppressed sexual selection by enforcing monogamy over 100 generations, with each male being allowed to court only one female. These males became suboptimal competitors in complex mating environments and also displayed reduced ability at forming associations in a non-sexual context (aversive olfactory learning). These findings provide support for the idea that male competition and/or female choice contribute to the evolution of male cognitive abilities.

This effect of sexual selection on cognitive evolution represents a different evolutionary scenario than the classic suite of studies on polygynous rodents, where selection is predicted to act on male spatial cognition because it allows finding and mating with as many females as possible during the breeding season (Gaulin and Fitzgerald 1986). Clint et al. (2012) re-examined this classic "range hypothesis" in a comparative study including 11 species from diverse taxonomic groups (fish, rodents, horse, primates and humans). While they underlined the robustness of the empirical evidence for male superiority over females in many spatial cognition tasks within multiple taxa, they found a non-significant correlation between the extent of this male superiority and home range dimorphism, which lends no support to an adaptationist account of these sex differences in cognition. Instead, they suggest that the evidence supports a "spill-over" hypothesis, where spatial ability dimorphism results from higher testosterone levels in males (which is known to improve spatial cognition) that has evolved for other reasons than reproductive benefits accrued from spatial ability. This exercise of considering alternative hypotheses is an important one: many phenotypic characteristics are likely not adaptations per se, but result from "side-effects" of other adaptations, developmental constraints or genetic correlations. The authors also warrant that finding fitness benefits of higher spatial ability in contemporary populations (as attempted by Spritzer et al. 2005) would not be sufficient evidence to conclude that a sex dimorphism in cognition is an adaptation to male scramble competition, because the adaptation process occurred in the past. A trait could have provided an adaptive advantage in the past but not show it nowadays (i.e. a vestigial trait). The time would now be ripe to re-examine this alternative hypothesis with a comparative approach making use of data collected in the past 10 years. Of particular interest is the finding of heightened female performance on an allocentric spatial memory task, relative to males, in brood-parasitic cowbirds (*Molothrus alter*), where only females search, parasitize, and revisit host nests, and thus show more complex spatial movement than males during the breeding season (Guigueno et al. 2014). This reverse sex difference in spatial ability is not consistent with the "testosterone spill-over" hypothesis, because testosterone levels are also higher in male than female cowbirds during the breeding season (Guigueno et al. 2016).

Social interactions among group mates have long been identified as a potential selection pressure on a range of cognitive abilities. The "social intelligence" (Jolly 1966) and "machiavellian intelligence" (Whiten and Byrne 1988) hypotheses propose that having to predict and adjust behaviour to that of other plastic agents (such as group members) should create positive feedback loops in the evolution of general cognitive skills (learning, memory, inference, etc.). The first hypothesis emphasized cooperation while the second highlighted competitive interactions; these two perspectives are most often treated together nowadays (e.g. Kulahci and Quinn 2019). While early work has focused on comparing species on some measure of brain size and group size (mainly primates, but also birds and mammals), few studies have examined intra-specific covariation in the social environment and cognitive abilities. This may be because sociality often covaries with ecological variables such as resource distribution (Overington et al. 2008), which can make 'social' predictions difficult to test without a confounding 'ecological' effect. In fact, many modern comparative studies find an effect of both aspects of the environment in studies on neural substrate evolution (e.g. Pollen et al. 2007; Reader et al. 2011).

A recent study on Western Australian magpies (*Cracticus tibicen dorsalis*) seemed to have pinpointed variation in group size that is independent of habitat characteristics, by making use of groups of 3–12 individuals living in urban parks. Ashton et al. (2018) showed that group size was positively correlated with performance on four different cognitive tasks, which themselves correlated together and were repeatable in the short term. This relationship was not present in very young birds tested at 100 days, but appeared at 200 and 300 days; it thus seems environmentally driven, pointing to the important role of developmental plasticity in determining cognitive phenotypes (Farrell et al. 2015). It is unclear at the moment what aspects of larger groups shape cognition in developing magpies; not much is known on the development of cognition in natural populations in general, due to logistical difficulties at conducting longitudinal studies in the wild. A laboratory experiment on young zebra finches (*Taenopygia guttata*) gave support to the idea that adult cognitive phenotypes will come to match the informational properties of the developmental environment (Frankenhuis et al. 2019). Birds having been reared in an environment where learning was rewarded (they experienced predictive cues for food) showed higher learning accuracy and faster decision-making in some cognitive tasks as an adult, compared with birds reared in the same conditions but who experienced non-informative cues (Rojas-Ferrer and Morand-Ferron 2020). The extent to which learning opportunities vary among individuals in the wild and affect cognitive developmental trajectories remain to be investigated.

Cognition & Fitness

Repeatability and Heritability

For a trait to respond to selection, it must have a genetic basis transmitted from generation to generation; a number of studies have supported this idea for cognitive traits. For example, artificial selection was used to select "maze-bright" and "maze-dull" rats, based on speed of completing a maze (Tryon 1942). While offspring of maze-bright rats indeed became more proficient at spatial tasks, they were also more motivated by food, and differed on other aspects of their phenotypes such as fear of open spaces (Searle 1949), highlighting that traits rarely evolve in isolation – and raising questions as to the actual target of selection in these experiments. On the other hand, researchers have computed heritability estimates for a small set of traits in a handful of species using approaches such as parent-offspring regression. For instance, moderate heritability of learning ability was found in honeybees, *Apis mellifera capensis* (Brandes 1988). However, most published estimates for cognitive performance are from lab populations (reviewed in Croston et al. 2015). Because heritability estimates are population- and context-specific (Sauce et al. 2018), this means we currently do not know if cognitive traits exhibit heritable variation in the wild. Challenges that need to be overcome include the difficulty of measuring cognitive performance in a large sample of wild individuals with enough known relatives to assess additive genetic variation while controlling for environmental effects (e.g. via the 'animal model'; Wilson et al. 2009).

A first step to evaluate the evolutionary potential of a trait is to measure its repeatability; this should always be reported in studies on individual differences in cognition (Griffin et al. 2015). Repeatability assesses the proportion of phenotypic variance due to among-individual differences, which is the level at which selection is expected to act. Finding no or very low repeatability suggests that the trait would show no heritability, and that variation is rather due to plastic adjustment in the behaviour of individuals over time, and/or measurement error. Repeatability can be assessed within-tasks using repeated trials (e.g. Morand-Ferron et al. 2015), or ideally, between repeated tests. The latter can be obtained by repeating the same task (temporal repeatability), or between different tasks that are similar enough to tap into the same cognitive processes (contextual repeatability) (Figure 8.2). Obtaining independent measurement of performance on tasks recruiting the same cognitive processes may often prove challenging however, because memory of the first solution can impact performance on the second test, leading to low between-task correlation in individual performance (e.g. Thompson and Morand-Ferron 2019). An encouraging finding on this front is that the meta-analytical temporal and contextual repeatability values for cognitive tests ($R=0.15$–0.28) in a range of species were found to be significant, albeit slightly lower than that of behavioural tests (Cauchoix et al. 2018).

Selection and Correlated Traits

Because humans value intelligence, and maybe because IQ correlates positively with various life outcomes in humans (e.g. education and longevity; Plomin and Deary 2015), it may be tempting to assume that cognitive abilities are positively associated with fitness in animal populations. However, cognitive processes are associated with a range of costs, such as high metabolic costs of brains and long developmental periods (Kuzawa et al. 2014), and/or time and energy invested in collecting, processing and using information (Dunlap and Stephens 2016). Thus, although cognitive processes such as learning and memory can help find food, access to mates, and avoid predators, it is the balance of the costs and benefits of a given cognitive ability that will determine if its association with fitness will be overall positive or negative (Figure 8.2). For instance, colour-based associative learning correlates positively with colony success in bees (Raine and Chittka 2008), and performance on a test battery is positively associated with reproductive success in female Western Australian magpies (Ashton et al. 2018), but colour-based reversal learning is negatively associated with survival after release in the wild in pheasants *Phasianus colchicus* (Madden et al. 2018). The latter example is an important demonstration that abilities which are not needed for survival and reproduction – pheasants had access to feeders in the wild after their release – may be selected against in the wild. The first study to estimate selection on a cognition-related trait has indeed revealed both associated costs and benefits; successful problem-solvers in wild great tits produced more chicks when they successfully nested, but they also had a higher likelihood of deserting the nest, resulting in no net selection for the trait (Cole et al. 2012).

The great tit problem-solving study cited above suggests that selection on cognition is impacted by correlated traits, as problem-solvers had lower nest success due to their higher rates of nest desertion. This effect was hypothesized to be due to lower tolerance of predation risk at the nest, which is supported by the results of a predator presentation experiment conducted on another Paridae species, the mountain chickadee *Poecile gambeli* (Kozlovsky et al. 2015). Investigating the correlations of cognitive traits with other types of traits, such as morphology, physiology, and behaviour (e.g. Chapter 25 Dingemanse and Reale 2021), is thus an important interdisciplinary endeavour, because selection rarely acts on traits in isolation. Recent findings in pheasants point to different patterns of correlation between tasks at the phenotypic vs. genetic level, suggesting it will be necessary to embrace a quantitative genetics approach to understand how various cognitive abilities and related traits are correlated at the genetic level (Langley et al. 2020).

An important task for cognitive ecologists is to identify which correlated traits need to be considered in conjunction with cognition to understand cognitive evolution (Figure 8.2). Some commonly studied confounding variables such as personality traits are routinely incorporated in studies on individual differences in cognition and could provide a useful first step. However, a recent meta-analysis reported inconsistent links between associative learning and personality traits related to novelty responses, suggesting that even those associations thought as pervasive might not generally cut across taxa or tasks (Dougherty and Guillette 2018). Another important question is the extent to which different cognitive abilities co-evolve (general intelligence) or are independently tuned to environmental demands (modular view of cognition). While most studies on humans find moderate to strong evidence for a positive correlation in performance across domains (associative, spatial, numerosity, causal inference, etc.), the evidence for a general intelligence factor in non-human animals is weaker, with low mean correlation in task performance across test batteries ($r=0.185$; Poirier et al. 2020). The extent of modularity may differ among taxa, as suggested by a significant species effect in the meta-analysis by Poirier et al. (2020). More research incorporating measures on different cognitive domains on the same set of individuals would help shed light on this issue, as studies targeting only one set of traits (e.g. only spatial cognition, or only inhibitory control) cannot inform this question of correlated evolution of cognitive traits. Moreover, the use of repeated measures (multiple tests per individuals for each cognitive domain) or related individuals (Sauce and Matzel 2018) will be necessary to assess correlations occurring at the level where selection is expected to occur (i.e. among rather than within-individuals, genetic rather than phenotypic; Langley et al. 2020).

Conclusions

Cognitive ecology is interested in uncovering links between the environment and cognition, with the aim of understanding how cognitive processes evolve in natural populations. While the role of environmental and social drivers of population or species-level differences in cognition can be examined with comparative studies, either through population comparisons or common garden experiments (Figure 8.2), a within-population approach comparing cognitive phenotypes to fitness has the potential to document natural or sexual selection in action in the wild (Figure 8.2). To understand the evolution of cognitive traits, we must not only estimate selection on traits of interest, but also uncover their heritability and genetic covariance with other traits (Figure 8.2). For instance, problem-solving success in wild great tits was associated with a higher number of fledglings among successful nests, but the heritability estimate of the trait was not statistically distinguishable from zero (Quinn et al. 2016). This suggests strong cohort effects, again pointing to the importance of the environment in shaping cognitive phenotypes in the wild (see also Vardi et al. 2020). Uncovering the links between heritability, plasticity, and fitness consequences of individual differences in cognition constitutes an important endeavour for future work.

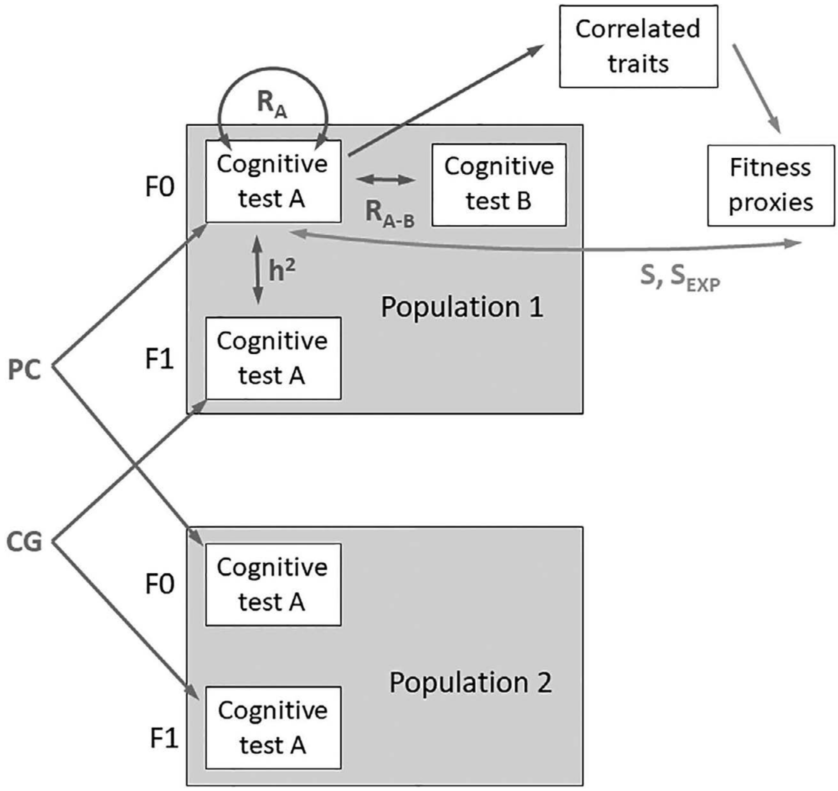

Figure 8.2 Schematic representation of some research approaches in cognitive ecology targeting intraspecific variation.

The boxes on the left represent two natural populations of the same species living in contrasting ecological/social conditions. For illustration purposes, I have classified approaches into three main themes: individual variation (dark grey: R_A, R_{A-B}, h^2), selection (light grey; S, S_{EXP}), and agents of selection (grey; PC, CG). (1) *Do individuals of a given population vary in cognitive performance, and does this variation correlate to other aspects of the phenotype?* Quantifying performance of the same individuals repeatedly on the same cognitive test (e.g. after a given delay) allows assessing temporal repeatability R_A. Measuring the performance of the same individuals on two different cognitive tests A and B assumed to recruit the same cognitive processes allows assessing R_{A-B}, the contextual repeatability of cognitive performance. Quantifying cognitive performance in individuals of known relatedness (e.g. using a pedigree), or in F0 and F1 generations (or ideally, F2 and F3 when using lab-raised individuals derived from wild ancestors) allows determining the heritability (h^2) of cognitive performance. Phenotypic and genetic correlations with other aspects of the phenotype (correlated traits) can be assessed to determine if selection acts directly or indirectly on cognitive traits. Heritability and the genetic covariance between traits can also be studied using artificial selection (not shown). (2) *Are cognitive traits under selection?* Natural variation in cognitive performance can be examined against fitness components (e.g. survival, mating success, fecundity, reproductive success) to quantify selection (S) in a given population. Experiments can be used to examine the adaptive value of information (S_{EXP}). (3) *Which selective agents act on cognitive traits?* Hypotheses on evolutionary causes of variation in cognition can be tested by comparing performance in individuals from multiple sites at two or more populations chosen for their contrasting ecological and/or social conditions (population comparison or PC). PC is a correlational approach; for a causal interpretation on agents of selection one can use experimental evolution (not shown). In common garden experiments (CG), offspring from contrasting populations are raised in identical conditions in the lab. This approach controls for among-population variation arising from exposure to the developmental environment, which is not the case when simply comparing phenotypes among populations (PC).

Adapted from Morand-Ferron, J. 2017. Why learn? The adaptive value of associative learning in wild populations. *Current Opinion in Behavioral Sciences*, 16: 73–79.

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PART 2

Behavioural Systems

9

HABITAT SELECTION AND ITS IMPORTANCE IN CONSERVATION BIOLOGY

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Introduction

The environment where an organism lives is rarely homogeneous. The vegetation, predators, parasites, food, water, and other resources and conditions needed by an organism to survive and reproduce usually vary spatially and temporally (Fretwell and Lucas 1970). This spatio-temporal variation of resources and conditions is one of the evolutionary drivers of animal locomotion abilities and of the development of their senses and certain cognitive capacities that allow them to survey, identify, select, and actively establish themselves in and use certain habitat types and to avoid others (Wiens 1976). Understanding how organisms use and select specific portions of their environments (i.e., habitat selection) is to learn some of the most basic aspects of their behavioural ecology and natural history. How and why animals select certain portions or resources of their surroundings, the role of experience in habitat selection, and how to study these aspects are some of the topics we will cover in this chapter.

Brief history of ideas and concepts

Determining which resources, or habitats, are selected, and the mechanisms to do so, are of particular interest for evolutionary and behavioural ecology because it would provide fundamental information about the nature of animals and how they satisfy their requirements for survival and reproduction (Manly *et al.* 2002). The study of habitat use and selection has a relatively long history. Grinnell (1917) referred to preferences and choices that animals make in their natural surroundings and enumerated a series of factors that limit the distribution and define the habitats of species. Svärdson (1949) suggested that intraspecific competition causes species to expand their range of habitats, making reference to the evolution of habitat selection and its dependence on density and interspecific competition. MacArthur (1958) later demonstrated that the coexistence of potentially competing species is facilitated by differences in microhabitat use. Fretwell and Lucas (1970) established the "ideal free distribution" concept, where individuals distribute themselves among several patches of resources of different quality to minimize competition and maximize fitness. This approach assumes that individuals possess perfect knowledge of the distribution of resources in the environment. Orians (1971) pointed out that, due to time constraints, birds seeking a place to breed usually make rapid decisions based on simple environmental cues rather than performing an exhaustive quality survey.

Wecker (1963) revealed that heredity and experience play a role in habitat selection. He documented that young animals exposed to particular stimuli are more likely to select habitats containing

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those stimuli when tested at older ages. However, during the selection process they also used signals and stimuli to which they had not been exposed before, suggesting an "innate" response as well. Hilden (1965) discriminated between proximate and ultimate factors affecting habitat selection, describing proximal factors as cues that animals use to determine the suitability of a site (e.g., composition of vegetation, presence of conspecifics), and fitness (i.e., reproductive success and survival) as the ultimate reason for habitat selection. Immelmann (1975) coined the term 'habitat imprinting', which refers to the importance of ontogenetic learning in habitat selection.

Early work on habitat selection was associated with studies of speciation, species distribution, range expansion, and niche theory (Rosenzweig 1981). Most recently, habitat selection studies are commonly focused on conservation issues, providing quantitative information on habitat requirements of populations of endangered species, modeling and projecting impacts of natural or human induced changes on their habitat (Caughley 1994). Habitat selection evolved into a unified statistical theory with the introduction of the concept of Resource Selection Functions (RSF—Manly *et al.* 2002), where resource selection is modeled as a function of covariates measured on resource units (e.g., pixels on a Geographic Information System—GIS), with the RSF value being proportional to the probability of use of each unit.

The hierarchical structure of habitat selection

Johnson (1980) described four "orders of resource selection". At the broadest level, or first-order selection, habitat selection defines the distribution or geographic range of a species. Within that range, second-order selection determines where animals establish their home-ranges. The third order of selection affects the intensity of use of habitat types within home-ranges. Finally, the fourth order refers to the selection or actual procurement of specific resources (e.g., food items, resting places) from those available in a habitat patch. It is important to define and understand the scale at which a study is conducted because the criteria for selection and the cues used by organisms may be different at each level. Thus, determining the scale of selection is a major goal of habitat selection studies, and considering more than one scale is recommended. A hierarchical view of habitat selection also makes possible the integration of studies on use and selection of habitat conditions and other resources, such as food, allowing an integration of analytical approaches.

Box 9.1 Terminology used in this chapter

Habitat—A distinctive set of resources (e.g., food, water, and cover), and environmental conditions (e.g., temperature, rainfall, presence or absence of predators and competitors, level of hunting pressure) that promotes occupancy by individuals of a given species or population, and allow them to survive and reproduce.

Habitat type—A particular kind or patch of vegetation, described as a spatial subset of habitat that is treated as a single homogeneous unit by the behaviour of an individual.

Habitat/resource selection—The disproportionate use of a resource, or habitat type, according to its availability.

Habitat/resource use—The quantity of resource or habitat type that is used in a fixed period of time.

Habitat/resource preference—The likelihood that a resource is selected if offered on equal amounts with others.

Home range—The area that an animal uses during its normal activities, such as foraging, resting, mating and caring for young, and excluding temporary movements such as migrations.

Territory—An area within the range of an animal or group in which it has priority of use, and from which other animals/groups are excluded by aggression, threat, or other signals.

Translocation—Human-mediated movement and release of living organisms from one area to another.

Reintroduction—A conservation translocation that implies the movement and release of an organism inside its indigenous range from where it became extinct.

How to assess habitat selection?

Selectivity can be assessed by the use or non-use of discrete resource units, or by the relative amount of use of those resource units. This division into units can occur naturally (e.g., limits between contrasting habitat types), or must be imposed by the researcher (e.g., quadrats in maps or pixels in a GIS) when habitat types occur along a continuous vegetation gradient, but considering the animals most-likely perception of those habitats. Resource units can be classified into categories (e.g., habitat types), or values of continuous variables can be assigned to each unit (e.g., mean shrub density, distance to water).

Usually, habitat selection is assessed using one of the following three approaches: (1) use-only data, (2) used vs. unused units, and (3) used vs. available units. They all involve evaluating a departure from a random use of spatial units, and only if a non-random use is found, is it merited to further explore habitat selection (Jones 2001). Use-only data include measurements of the amount of time spent by animals in defined available habitat types or through a count of the number of occasions that a unit is used (e.g., Di Bitetti *et al.* 2000). Counts of use can be applied to a survey on a study area that is divided into a given number of plots, on which individuals or groups are counted, and where the probability of detection is the same throughout the study area (e.g., Månsson *et al.* 2011). Used vs. unused units occur when the presence and absence of use can be recorded with certainty (e.g., Boyce *et al.* 2002). In the case of used vs. available units, one of the most widespread methods in habitat selection studies of tagged individuals, available units should be generated as pseudo absence-data (e.g., Di Blanco *et al.* 2015, 2017a). It is important to consider that the estimation of the amount of use or avoidance does not reveal the reasons why a particular habitat type is positively or negatively selected but is a starting point for further studies (Manly *et al.* 2002).

Resource Selection Functions

Manly *et al.* (2002) highlighted that a unified statistical theory is needed for the analyses of habitat/resource selection studies, and that the concept of a resource selection function may fulfill this premise. Resource selection functions (RSF) are mathematical models that estimate the degree to which resources or environmental conditions are "selected" or "avoided" by a particular individual or population in a given area and time period. They use a linear combination of weighted values (coefficients) of predictor variables (covariates) to estimate resource selection in regression models. Any possible set of covariates (physical, biological, chemical) of potential predictive value (i.e., that animals can use to exert selection of habitat types or conditions) can be considered in RSFs, and different combinations of covariates can be evaluated among a large set of competing models (e.g., Burnham and Anderson, 2002). The strength of the contribution of each individual covariate (i.e., its importance) to the overall model predictions can be estimated. Model predictions can be spatially explicit and plotted on maps.

There are several varieties of RSF. Resource Utilization Functions (RUFs—Marzluff *et al.* 2004) express the correlation between spatially defined resources and the utilization distribution (van Winkle 1975) in a defined area, such as a home range. Step Selection Functions (SSFs—Richard and

Armstrong 2010) are a relatively recent derivation of RSFs, being a promising approach for estimating the strength of habitat selection by animals moving through a landscape using especially high frequency spatially dependent GPS location data.

What influences habitat selection by animals

The idea that animals somehow perceive the correct configuration of habitat required for their survival is among the most accepted assumptions behind habitat selection studies (Morrison *et al.* 1992; Manly *et al.* 2002). The challenge is to see the world as animals do, and to identify which characteristics of the habitat they perceive as important. Variation in these characteristics is usually associated with variation in fitness. The relationship between animals and their environments should be understood in the context of past ecological relationships and the evolutionary history of the species. However, it is important to keep in mind that relationships that shaped habitat selection in the past may not be impacting the animal in the present (e.g., predators that enabled certain anti-predatory adaptations may now be extinct). Furthermore, new conditions for which animals are not adapted might now be impacting habitat selection (Morrison *et al.* 1992). Population densities, competitors, predators, prey availability, habitat patch sizes, inter-patch connectivity, mates, presence of offspring, and the spatial distribution of resources are some of the long list of factors that may contribute to habitat selection (Johnson 1980; Manly *et al.* 2002). The relative importance of these factors to habitat selection will depend on the interaction between the characteristics of the habitat and the species' or individual's intrinsic features (e.g., movement capacity) and previous experience (e.g., previous exposure to predators), which is reflected in inter- and intra-population variation.

Habitat selection in dispersing animals

Habitat selection studies on dispersing animals are informative because dispersal is a critical life history stage when habitat selection has the highest impact on fitness. Since important questions are where they will establish a stable home range and how they will use it, the study of habitat selection in dispersing animals is usually focused on intermediate spatial scales (second and third order selection). Studies of habitat selection in dispersing animals are centered on the processes by which individuals search for and select new locations to establish their home ranges and on the consequences of those processes for the distribution, density, and fitness of individuals in different habitats (Hilden 1965; Stamps 1994). Contrary to classical habitat selection theory, that assumes that animals possess perfect knowledge on the quality of habitat types available (Fretwell and Lucas 1970; Manly *et al.* 2002), natal dispersers may lack the time or energy required to perform a reliable assessment of the new habitats encountered (Stamps *et al.* 2005).

The experience in natal habitats and conspecific attraction are two behavioural mechanisms that play important roles in habitat selection in dispersing animals (Stamps 2001). The physiological and behavioural tools required by dispersers to locate, evaluate and select a new area in which to settle are often acquired in their natal habitat (Stamps 2001). The experience at early development can improve skills in anti-predator behaviour (Curio 1993), foraging (Eadie 2015), social interactions (White *et al.* 2010), and immunity to certain pathogens (Wilson-Rich *et al.* 2008). Therefore, it is expected that dispersing individuals would perform better if they selected habitat types similar to those found in their natal range (Stamps 2001). The exposure to a given habitat type at a sensitive period of development early in life, known as habitat imprinting, increases the likelihood that a dispersing animal will select it to settle in a new location (Immelmann 1975). Natal habitat preference induction (NHPI) occurs when the experience of a disperser in its natal habitat biases its preferences for certain habitat types in the new environment, independently of a sensitive period of development (Stamps and Swaisgood 2007). Animals exhibiting NHPI are expected to prefer habitat types that possess characteristics or cues found in their natal habitat. Sometimes these cues are directly related to fitness (e.g., predator presence or abundance), but animals often use indirect cues, that may or may not be correlated with habitat quality and fitness (Stamps and Swaisgood 2007).

Conspecific attraction is a term that relates the positive associations between habitat selection and the presence of conspecific cues (Buxton *et al.* 2020), and occurs when the presence of conspecifics increases the chance that an animal will settle at a given location (Stamps 1991); see also "Social Contextual Influences on Behaviour", Chapter 24. This contradicts one of the assumptions of the ideal free distribution (Fretwell and Lucas 1970): that individual fitness declines as a function of the density of conspecifics. Even solitary and territorial animals may benefit from the presence of conspecifics when living at low to moderate densities (Hilden 1965). Those benefits may include a decrease in predation risk (Drakeley *et al.* 2015), more efficiency in expelling intruders (Meadows 1995), and increased access to mates (Clark 1998). Heterospecific attraction has also been described. This occurs when individuals of other species serve as cues of habitat quality and the benefits of interspecific aggregation outweigh potential costs of interspecific competition (Thomson *et al.* 2003).

Habitat selection in solitary vs. social animals

Social evolution has been widely explained by resource distribution and/or predation risk. According to the resource dispersion hypothesis (RDH), when resources are patchily distributed in space and/or time it is possible for one range to sustain several individuals satisfying their resource needs without imposing large costs on each other, which can result in the formation of spatial groups (Johnson *et al.* 2002). Conversely, habitat selection may be affected by group size, as the rate of resource acquisition and predation risk often change when an individual joins a group (e.g., Bednekoff and Lima 1998; Fortin *et al.* 2009). Information derived through social foraging (i.e., public information) can decrease uncertainty about the quality of the environment, thereby increasing efficiency in habitat selection (Fernández-Juricic *et al.* 2006). On the other hand, collective vigilance, cooperative defense, and dilution and confusion effects (Bednekoff and Lima 1998) cause predation risk to decrease with group size, which in turn may favor the selection of habitat types with higher predation risk.

Habitat selection in translocated animals

The success of translocations depends on released animals settling in unfamiliar areas. As early life experience might affect future habitat selection patterns, concepts such as habitat imprinting and NHPI can be applied by managers to enhance translocations success. However, several differences need to be recognized between natural dispersers and translocated animals. Dispersers leave their original site at a particular age and, often, at a particular season, while translocated animals are freed into a new area, at different life stages and times of the year (Stamps and Swaisgood 2007). Translocated animals may be captive-born or captive-reared and are released without the necessary experience into a new environment.

The post-release period is critical because translocated animals may immediately depart from the release site to search for their original location ("homing behaviour"—Joslin 1977) and thus, they may face higher mortality rates and other effects (e.g., weight loss) with negative fitness consequences (Sarrazin and Legendre 2000). In addition, it may become complicated to monitor them (Seddon 1999). According to NHPI, these long-distance movements away from release sites may occur because animals prefer to settle in familiar habitat types, rejecting novel areas lacking the cues found in their area of origin (Stamps and Swaisgood 2007). Therefore, relocated animals can be induced to remain in purportedly favorable areas by establishing familiar cues in the release sites. This idea has been already adopted with success in "soft releases" where animals are confined in enclosures at release sites for given periods of time before release (Scott and Carpenter 1987). During this period they can become familiar with environmental features or critical resources or cues can be provided to reduce the chances of rapidly leaving the area.

Captive-born and captive-reared animals usually have a lower performance and suffer higher mortality than wild-reared animals when they are released into a new habitat (Fischer and Lindenmayer 2000). Insights from habitat selection theory may help conservation managers to increase the success of translocation projects (Stamps and Swaisgood 2007). The chances of success can be increased by incorporating elements of the natural environment into captive environments, by environmental enrichment (Swaisgood and Shepherdson 2006), and by providing experiences that can train animals in specific survival skills, such as offering the same type of food items that they are likely to encounter after release, shelters comparable to those that are likely to encounter in the new habitat, or experiencing predator exposure (e.g., Griffin *et al.* 2000). On the other hand, animals raised in captivity under favorable conditions may learn to identify conspicuous cues and will then prefer to settle in areas that contain those cues after being released. The temporary provision of support after release (e.g., food, shelter, vaccines, etc.) may also increase the success of translocations.

Habitat selection in reintroduced giant anteaters

The giant anteater *Myrmecophaga tridactyla* (from here on anteater) become extinct in the Iberá Wetlands ecoregion of North-eastern Argentina around the middle of the twentieth century. As part of an ecosystem restoration project an anteater population was reintroduced to this region (Zamboni *et al.* 2017). We here describe the process of habitat selection by reintroduced anteaters at Iberá (Di Blanco *et al.* 2015) and we compare these patterns with a wild population in a similar, but distant, site at the Pantanal of Brazil (Di Blanco *et al.* 2017a). This description will serve to exemplify and discuss some of the concepts and processes described in previous sections and their potential applications.

The giant anteater is the largest of living xenarthrans, with a mean weight of 33 kg. Anteaters are mostly solitary, except during the breeding season or when females are carrying their young. Across its vast range, anteaters occupy a diverse array of habitat types including grasslands, savannahs, and forests. Their diet consists almost entirely of ants and termites (Gaudin *et al.* 2018). Their low metabolism when compared with other mammals of similar size makes giant anteaters sensitive to extreme temperatures (McNab 1985). This limitation seems to influence anteater activity patterns and habitat selection, accommodating its diel activity to local conditions or experience (Di Blanco *et al.* 2017b) and using vegetation cover as protection from extreme temperatures (Camilo-Alves and Mourão 2006).

Anteaters establish well defined home ranges that can overlap those of neighboring individuals (Shaw *et al.* 1987; Mourão and Medri 2007). Territorial displays and marking of trees suggest some degree of territoriality (Shaw *et al.* 1987; Braga *et al.* 2010). In addition, captive reared giant anteaters have a low mortality rate after being released in the wild, and they are relatively easy to capture and handle during post release controls and monitoring (Jiménez-Pérez *et al.* 2016). These characteristics make giant anteaters a good model for translocations and habitat selection studies.

Study areas and methods

The reintroduction was carried out at the Iberá Nature Reserve (INR), a 13,000 km^2 multiple use protected area that includes a diverse mosaic of vegetation units constituted by the Iberá marshland and surrounding terrestrial ecosystems. The most common land use within the INR is cattle and sheep ranching. The reintroduction was carried out on a 124 km^2 private reserve dominated by grasslands and savannahs and including small and narrow patches of continuous hygrophilous forest along temporary streams. There were no cattle or dogs at the reintroduction site. This reserve shares a boundary with private properties under traditional cattle production, a main dirt road, and marshlands (Figure 9.1). Anteaters were released away from the boundaries of the reserve, but according to their typical daily displacements and home range sizes, they could reach other properties within a day

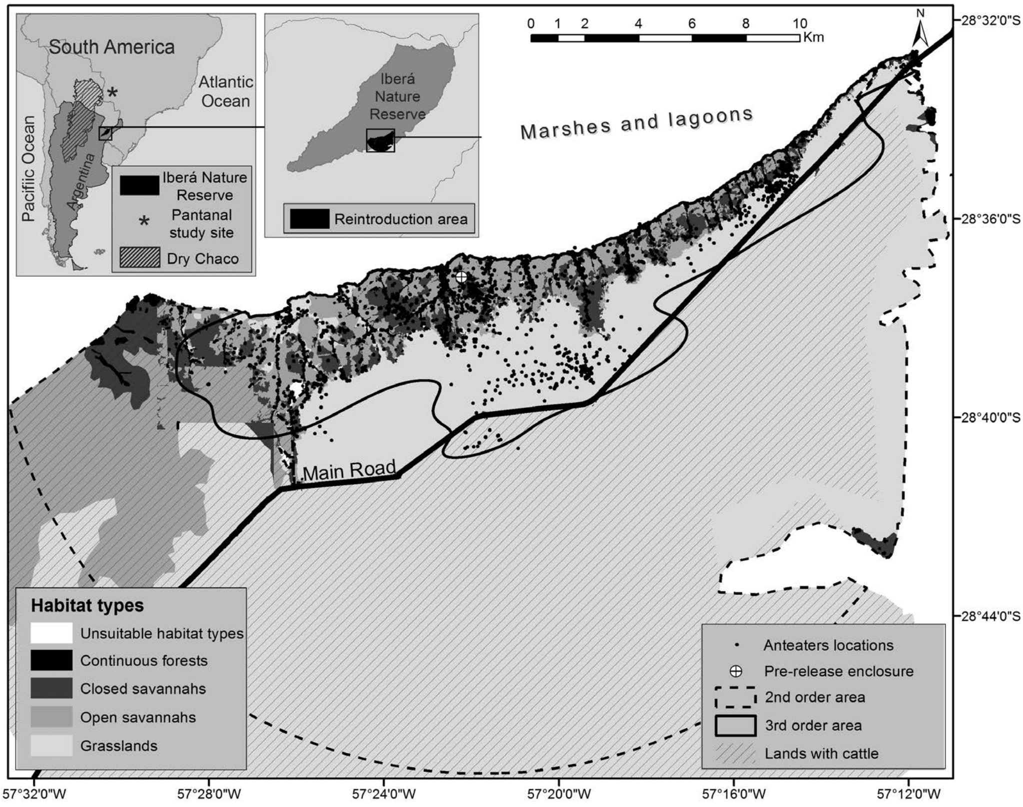

Figure 9.1 Study area at Iberá Nature Reserve, Argentina, showing the scales of analysis, habitat types, and anteater locations. Modified from Di Blanco *et al.* (2015).

or two. The Pantanal study site is a private ranch where cattle production is extensive and receives small groups of eco-tourists for wildlife watching. There are only small internal tracks and roads in the area and hunting is uncommon.

At Iberá we first classified areas according to the presence or absence of cattle. At both sites we classified areas into habitat types potentially suitable or unsuitable for anteaters. Unsuitable habitat types included aquatic and human disturbed ecosystems (e.g., marshes, human settlements). We classified suitable habitats into four types: (1) Grassland, constituted by temporary flooded tall grasslands; (2) open savannah with sparsely distributed palms and trees; (3) closed savannah with higher density of trees, including small forest or bushland patches; and (4) continuous forests (Di Blanco *et al.* 2015). Continuous forests cover nearly 40% of the study area in Pantanal but less than 5% in Iberá (Di Blanco *et al.* 2017a).

Between October 2007 and December 2013, 31 anteaters were released in Iberá. Reintroduced individuals were one to eight years old when released and were born at different sites of the Argentinean Dry Chaco region (Figure 9.1). Most animals were brought from foster families at an early age (from days to a few months old) and hand-reared in captivity in nursery facilities until they were the proper size to be released (Jiménez-Pérez *et al.* 2016). Captive-reared animals were kept in acclimation enclosures at the release site for up to two months and then soft-released. Eighteen of the 31 released animals were monitored via VHF-telemetry for a minimum of six months (Di Blanco *et al.* 2015). Only the adults (N=9) were used in the comparative study of habitat selection with wild animals at Pantanal. In the Brazilian site 10 adult anteaters were captured and released in site with GPS-tracking devices, and their locations were recorded between 2013 and 2015 (Di Blanco *et al.* 2017a).

In Argentina, individuals were located by following the radio signal until the animal was seen or heard. The activity sensor of the transmitters allowed us to know if the animal was resting or active before approaching to record its location. Locations were then collected with a hand-held GPS along the 24-h day period, ranging from once per hour to once every 30 days (Di Blanco *et al.* 2015). GPS locations in the Brazilian site were taken around the clock as frequently as every 20–40 min. Since data at each site were taken at different intervals, we randomly selected one location per day to make data from Pantanal and Iberá comparable (Di Blanco *et al.* 2017a).

Habitat selection by reintroduced anteaters was studied at two spatial scales that represented Johnson's (1980) second and third order of resource selection. We defined a second order of selection surface (available area where they could potentially establish home ranges) based on the maximum movement capacity of individuals observed during the study. The available area for third order selection was determined by a home range estimated for the population as a whole (Figure 15.1, Di Blanco *et al.* 2015). At Pantanal we studied and compared habitat selection at the third order of selection only, using the same procedures used at Iberá. We compared anteaters' used locations to a set of available locations randomly generated within the different scale surfaces to estimate the maximum-likelihood values of model coefficients in RSF. We included habitat types and distance to forest edge as predictor variables. For the reintroduced population exclusively, we also included the distance to the main road as predictor variable, and independently modeled habitat use for adults and juveniles. Distance to human settlements, and distance to permanent water ponds were also used as predictor variables in Pantanal.

Lessons learned

Independently of the scale of analysis, vegetation structure was an important predictor of habitat selection by reintroduced anteaters, with the higher probability of occurrence concentrated in the continuous forest or its proximity. Given the paucity of forests in Iberá, less than 4% of the landscape has a good-to-high likelihood of giant anteaters' occurrence at the second order selection scale of analysis (Di Blanco *et al.* 2015).

In contrast to Iberá, Pantanal forests were used according to their availability (Di Blanco *et al.* 2017a). The availability of forests in Pantanal is much higher than in Iberá (40% vs. 5% of available habitat types) which may explain this lack of selection for them. This is an important lesson learned from this comparative study: the relative availability of habitats may bias estimates of their selectivity. Anteaters probably do not perceive forests as less important in Pantanal, but their higher availability reduced their selectivity. Thus, erroneous conclusions may be drawn from habitat selection studies based on a use-availability approach by ascertaining that critical habitat types are not important when they are highly available.

Human activities can modify vegetation structure and produce stimuli that can affect habitat-selection by anteaters. We a priori defined cattle ranching as an important categorical variable, but less than 2% of anteater locations were recorded in areas with cattle (see Figure 9.1). Lands with livestock were so highly avoided by anteaters that we considered it unnecessary to include this variable in the models. The strong avoidance of lands under cattle management could be explained by an increased perception of predation risk due to the simplified vegetation structure that results from grazing and the frequent use of fires used to regrow pastures. In addition, dogs and wildlife hunting are common in lands under cattle ranching. Most reintroduced anteaters were recovered at an early age after hunters with dogs killed the anteater mother (to avoid injures to the dog). These early-age experiences could have generated some sort of imprinting, with certain stimuli being recognized and used by anteaters to negatively select certain habitats when establishing home ranges.

Traditional cattle ranching could have been one of the causes for the local extinction of anteaters in Iberá. Anteaters coexist with cattle in the Pantanal wetlands, where the hunting of wildlife is rare, and forests are not a limiting factor. At Iberá, in the margin of their continental distribution, the abundance of anteaters could have been naturally low, for which the presence of strict protected areas with forests seems to be the key to the successful reintroductions of anteaters and their future persistence in the region (Di Blanco *et al.* 2015).

The age, sex or rearing conditions of reintroduced individuals may have contributed to intra-population variation in habitat selection patterns and may be related to the success of species reintroduction programs. Reintroduced juvenile anteaters showed lower habitat selectivity than adults, probably due to their inefficient searching and underdeveloped foraging skills or to their lower competitive abilities that restricted them to less preferred habitats (Di Blanco *et al.* 2015). Home ranges of males were larger than those of females (Di Blanco *et al.* 2017a), something congruent with the typical mammal pattern (McLoughlin and Ferguson 2000), but we were not able to assess sex differences in habitat selectivity due to sample size constraints. Despite these age and sex differences, individuals of both classes were able to establish home ranges and reproduce in the new habitat, although some

Figure 9.2 A reintroduced female with cub after her second release.

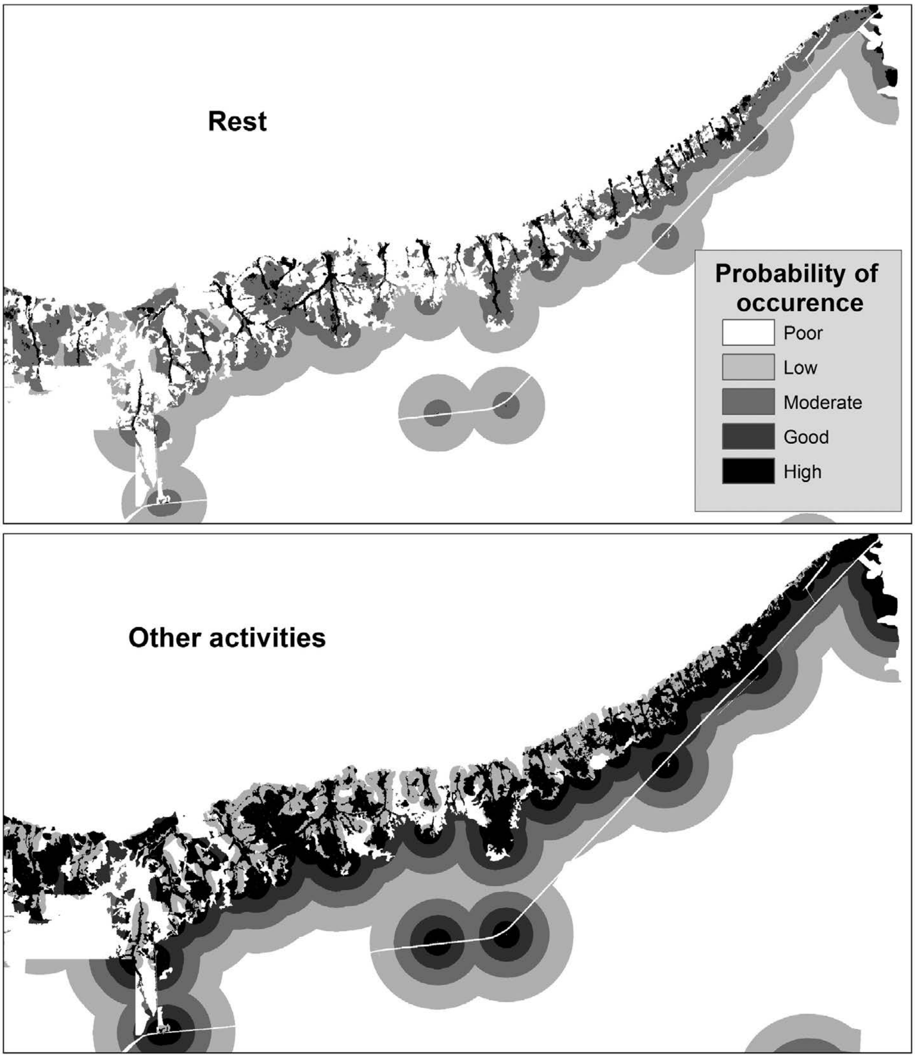

Figure 9.3 Probability of occurrence of anteaters at Iberá during resting (top) and other activities (bottom) according to a RSF model based on selected covariates. Models were based on data from nine adult anteaters released in Iberá Nature Reserve, Argentina. Modified from Di Blanco *et al.* (2015).

individuals required some support and all benefited from management practices we learned, sometimes the hard way.

At the beginning of the reintroduction project, when there was no established anteater population yet, individuals were kept in an acclimation pre-release enclosure, but were later immobilized, transported, and released at a different location and at different times of year. Others were hard-released without acclimation time in-site. Two of those first reintroduced females produced long distance (>25 km) movements from the release site. They were both recaptured and returned to the release site a few months later, but one of them left the release site again and was never recovered. The other one established her home-range near the release site, where other individuals were being recently released. After her second release she was seen with a male and next year had an offspring (Figure 9.2). This suggests that the presence of conspecifics, and especially mates, is important to anchor individuals at the release site. Releasing pairs seemed to increase the permanence of individuals near the release site and limited initial long-distance movements (Zamboni *et al.* 2017). Later individuals were also soft-released, where animals received supplemental food (the same mixture used during hand-rearing) within enclosures and during the first few months after release. Mortality and weight loss of released animals was higher in winter for which food supplementation was later routinely enforced during this season. Releases were also avoided during this time of the year. The use of soft-releases at the right time of the year with familiar food supplementation after release may have also prevented long-distance movements and improved chances of survival of subsequently released animals (Zamboni *et al.* 2017).

Habitat selection studies should use unbiased sampling protocols. For example, giant anteaters are mostly diurnal during colder months and mostly nocturnal during hot months (Di Blanco *et al.* 2017b). If radiolocations had been recorded only during daylight hours (as is the case in most field studies), seasonal differences in habitat selection would have emerged that may simply reflect habitat preferences for resting vs. foraging. We surveyed locations randomly into the 24-h cycle to avoid this bias (Di Blanco *et al.* 2015). Additionally, resource availability and habitat selection patterns may vary with seasons (Schooley 1994). In our case it was possible to evaluate habitat selection patterns both by activity (i.e., using resting and other activities locations), as well as by season, and we found clear differences (Di Blanco *et al.* 2015). Forests were highly selected for resting in relation to other habitat types, while during other activities (e.g., foraging) selectivity of other habitat types increased greatly (Figure 9.3). Thus, depending on the research question, pooling information across time (e.g., seasons, moon or daily cycles) or subpopulations may result in erroneous inferences (Manly *et al.* 2002). Studying habitat selection at different spatial and temporal scales can bring clarity and a broader and more comprehensive knowledge of ecological theory and the natural history of a species.

Conclusions

Understanding how and why animals select specific portions of the environment provides fundamental information about how animals satisfy their requirements for survival and reproduction. Habitat selection can be assessed with use-only data or by relating used vs. unused or available units. Defining the scale of selection is an important decision in habitat selection studies because the availability of resources or habitat types under study depends on it. The use of resource selection functions is growing and constitutes an important tool to model the effect of variables that may influence habitat selection.

Observed habitat selection patterns do not always match fitness outcomes, which have been explained by anthropogenic, methodological, ecological, or evolutionary discordances (Chalfoun and Schmidt 2012). This is probably because determining the cues perceived and used by animals to select habitats and resources is not easy, especially in field studies. Future studies should concentrate on this, and on evaluating the degree and the sources of inter- and intrapopulation variation in habitat selection patterns. This is particularly important given the uncertainties associated with ongoing climate change and its effect on future global environmental patterns. Habitat selection studies will help us understand how organisms respond to these changes. Applications of habitat selection theory and practice are growing, especially in the flourishing fields of conservation biology and restoration ecology, which are increasingly using translocations as a tool for environmental remediation.

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10

WHERE, WHAT AND WITH WHOM TO EAT

Towards an integrative study of foraging behaviour

Mathieu Lihoreau and Tamara Gómez-Moracho

Introduction

Foraging is the process by which animals obtain food to sustain their metabolism, grow and reproduce. This encompasses phases of exploration to locate food patches, as well as phases of food selection, processing and consumption. Foraging behaviour can take various forms depending on the animal's locomotion mode, feeding guild and ecological niche, from the passive filter feeding of molluscs, to the active hunting of mammal predators, and the fungus growing of ants. In some species, foraging is an individual activity, whereas in others, it involves tight cooperation between thousands of individuals.

How do animals manage to locate food in complex natural environments? How do they choose between alternative resources to meet their physiological needs? And how do they deal with competitors or predators? Over the past decades, these different facets of foraging behaviour have been studied using approaches from biology, ecology, physics and mathematics, resulting in separate bodies of theory across disciplines of behavioural research (for reviews see: Pyke, 1984; Stephens, Brown and Ydenberg 2007; Sumpter, 2010; Simpson and Raubenheimer, 2012). The time has come to integrate these approaches into a common framework to develop a more comprehensive understanding of animal foraging decisions.

Here, we first review some of the most influential conceptual frameworks used to study these facets of animal foraging behaviour by behavioural ecologists, nutritional ecologists and ethologists. We then explain the need to better integrate these approaches into a common framework, by considering the multiple dimensions of animal foraging decisions and their broader impact on the environment. Such integration can facilitate comparative analyses between species and ecological contexts. It can also shed light on broader scale ecological phenomena such as species assemblages and ecosystem services. We illustrate this idea using recent studies in bees.

Influential frameworks

Foraging decisions encompass many different facets of an animal's behaviour that have often been studied separately using dedicated theoretical and experimental approaches. Below we describe some of these approaches that are still dominant in modern foraging research.

Optimal foraging theory

How should animals move between food patches and choose food items? This question has intrigued behavioural ecologists since the mid-1960s, leading to one of the most popular theories in

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behavioural research: Optimal Foraging Theory (OFT) (for reviews see Pyke 1984; Stephens, Brown and Ydenberg, 2007).

OFT is an application of economics models, assuming that the foraging patterns optimising the fitness cost/benefit balance for animals will be selected through natural selection. Since animals often cannot do two things at once, increasing the time spent on looking for food reduces the time available for other essential activities, such as mating, defending resources or avoiding predators. The functional approach of OFT considers that individual animals should exploit foods in such a way that they select the most profitable resources per unit of search effort, thus in effect optimising their net energy gain (Kamil, Drebs and Pulliam, 1987). To this end, OFT uses techniques of mathematical optimisation and modelling to make predictions about animal foraging behaviour. Models can differ in the behavioural decision they consider (e.g. patch use, prey choice, habitat use), in how they consider the environment (e.g. sequential encounter with food resources, simultaneous encounter), and in which currency they maximize (e.g. rate of net energy intake, probability of survival).

The "marginal value theorem" is a classic example of an OFT model tackling the problem of when an animal should leave a food patch when the environment potentially contains others that are more rewarding (Charnov, 1976). Think of a bird searching for insect preys. In the model, the rate of returns for the bird is assumed to decrease with time spent in the patch due to depletion effects. In a plot of the returns as a function of time spent foraging in the patch, the curve starts off with a steep slope which gradually levels off as insects become harder to find. Additionally, the bird loses foraging time and expends energy to travel to new potential insect patches. The average time spent searching for a patch can be included in the model by assuming that patch exploitation starts after a given amount of time spent travelling. In this simple approach, graphically, the amount of time optimising net energy gain the bird should stay in the patch before leaving for a new patch is given by the point where the line extending from the zero value on the time axis touches the returns curve.

Although OFT models initially focused on the foraging decisions of individual animals, optimisation of foraging behaviour can also have important consequences at the population level. For instance, the "ideal free distribution" is another popular OFT application to predict how foragers in a population should distribute themselves among available food patches in order to minimise competition and maximise individual energy gains (Fretwell and Lucas, 1970). The theory states that the number of individual animals that will aggregate in different food patches is proportional to the amount of energy available in each food patch.

Several experimental studies have provided qualitative support for predictions of OFT across a wide range of animals and thus demonstrate its usefulness (Stephens, Brown and Ydenberg, 2007). However, in many cases, the behavioural results did not quantitatively match model predictions, thus raising criticisms regarding the validity and the limitations of OFT (Pyke, 1984). In particular, OFT models often rely on unrealistic assumptions. Examples involve that (1) an individual animal has perfect knowledge of its environment (i.e. omniscience); (2) an individual's fitness depends on its behaviour while foraging; (3) the relationship between foraging behaviour and fitness is known (i.e. currency of fitness); (4) there is a heritable component of foraging behaviour; (5) the evolution of foraging behaviour is not prevented by genetic constraints; (6) the evolution of foraging behaviour is not severely limited by functional constraints (e.g. morphology, physical properties); (7) foraging behaviour evolves more rapidly than the rate at which the relevant conditions change.

Despite these limitations, OFT is still a dominant paradigm in behavioural ecology, improving assumptions and refining models as new data comes to light. Efforts in further developing its applications have led to the development of exciting new lines of research, for instance with the study of how climate change may impact on the evolution of foraging behaviour (Wosniack *et al.* 2017; Calgano *et al.* 2019)

Nutritional geometry

What should animals eat? This question has raised the interest of nutritional ecologists in the mid-1990s, based on the observations that beyond energy intake maximisation, animals primarily choose food resources that best meet their needs in specific nutrients (for a review see Simpson and Raubenheimer, 2012). In particular, concepts of Nutritional Geometry (NG, also known as the "Geometric Framework for Nutrition") have been increasingly used to study how individuals compensate for nutrient deficits in foods and how any impairments in doing so affect fitness traits.

NG uses state-based models in which individual animals, foods and their interactions are represented graphically in a geometric space (nutrient space) defined by two or more food components (typically, but not necessarily, the macronutrients protein, carbohydrates and fat) (see theoretical examples in Figure 10.1). Foods are represented as radials through the nutrient space at angles determined by the balance of the component nutrients they contain (nutritional rails). The animal's nutritional state is a point that changes over time. As the animal eats, its nutritional state changes along the nutritional rail for the chosen food. The functional aim for the animal is to select foods and eat them in appropriate amounts and ratios to reach its optimal nutritional state (intake target). Knowing the position in the nutritional space of an individual's nutritional state and its intake target provides a basis for making predictions about its physiological, behavioural and fitness responses to the nutrient supply in the environment. For instance, an animal can reach its intake target by eating a single nutritionally balanced food (Figure 10.1A) or by mixing its intake from two or more nutritionally complementary foods (Figure 10.1B). If the animal is restricted to a nutritionally imbalanced food, it must reach a compromise between over-ingesting some food components and under-ingesting others (Figure 10.1C), for instance by minimising the Euclidean distance between its nutritional state and its intake target (e.g. closest distance rule of compromise in Figure 10.1C).

NG models have initially been designed to describe how individual animals (i.e. locusts) manage to balance their acquisition of protein and carbohydrates from artificial diets in the lab (Raubenheimer and Simpson, 1993). In recent years, however, this approach has also proved incredibly successful to study broader aspects of animal physiology, behaviour and ecology, and to address problems in applied nutrition, for instance to improve diets for domestic animals, characterise the nutritional needs of

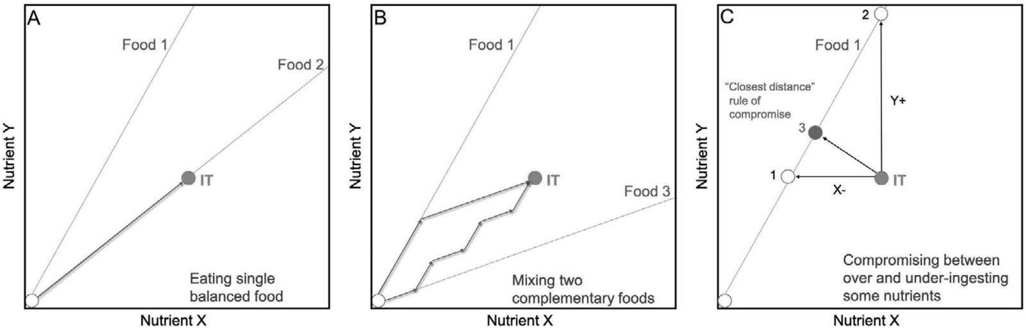

Figure 10.1 Nutritional Geometry models for a hypothetical animal. Nutritional rails (grey lines) represent the ratio of two nutrients (X and Y) in foods. The white dot is the animal's nutritional state. The grey dot is the animal's intake target (IT). (A) Food 1 is nutritionally imbalanced (contains a different nutrient ratio to the IT). Food 2 is balanced (contains the same nutrient ratio as the IT). The animal can reach its IT by exclusively eating Food 2 (arrow). (B) Foods 1 and 3 are individually imbalanced but complementary (fall on opposite sides of the IT). The animal can reach its IT by combining its intake from the two foods (see different possible sequences of arrows). (C) The animal is restricted to a single imbalanced food and can: (1) satisfy its needs for Y but suffer a shortfall of X; (2) satisfy its needs for X but over-ingest Y; (3) suffer a moderate shortage of X and excess of Y. Modified from Simpson and Raubenheimer (2012).

endangered species or explore ways to improve health. Remarkably, concepts of NG have revealed that we humans have a specific appetite for proteins, and that this appetite coupled with the dilution of protein in modern diets is a major driver of obesity due to the over-ingestion of carbohydrates and fat (Saner *et al.*, 2020).

Concepts of NG have also been extended to study how animals forage and balance their diets collectively, as this is the case for instance in social insects, such as ants and many species of bees, in which some individuals (the foragers) must collect foods to meet their individual nutritional needs as well as the diverging needs of all other individuals in the group (e.g. non foraging workers, queens, brood) (Lihoreau *et al.*, 2018). The same principles have been used to study nutritional relationships between animal species, for instance in host-parasites or host-commensal interactions (Wong *et al.*, 2017).

Collective animal behaviour

How should social animals forage? This question has raised the interest of ethologists and systems biologists in the 1990s, who used concepts from statistical physics to study how complex collective behavioural patterns emerge in animal groups from local interactions between individuals (for a review see Sumpter (2010)). Think for instance of a fish school, a bird flock, a herd of mammals, an insect swarm, or a group of humans looking for food. In many of these social entities, the collective acquisition and processing of information related to food location and quality provide important benefits to individuals, enabling them to make faster and more accurate foraging decisions in groups than alone, a phenomenon known "swarm intelligence". Colonies of social insects provide striking examples of how animals can make efficient collective foraging decisions based on relatively simple social interactions. Through information transfer, in the form of chemical cues (e.g. ant trail pheromones) or physical contacts (e.g. honey bee waggle dance), colonies can often find the best available food resource among many alternatives, for instance by choosing the patch with the highest concentration of sucrose solution (Beckers *et al.*, 1990) or a single key nutrient (Hendriksma and Shafir, 2016).

The mechanistic approach to the study of collective animal behaviour combines behavioural observations of individuals and groups with mathematical modelling (typically but not exclusively individual-based models), to show that many collective behaviours can be described in terms of three key principles: (1) quorum responses, in which the probability of an animal taking a particular action varies non-linearly with the number of individuals already performing it; (2) positive feedbacks, when repeated interactions between individuals amplify this probability; and (3) negative feedbacks, when repeated interactions between individuals reduce this probability. Collective foraging decisions typically arise from self-organisation, through a cascade of local interactions with no need to invoke global information or leadership (Camazine *et al.*, 2001). These principles have been identified in a wide range of group types and species, from the temporary aggregation of cockroaches looking for a piece of bread, to long-term colonies of millions of ants cooperating for exploiting a tree (Sumpter, 2010), but also between individuals of different species, as for instance maggots developing on a carcass (Boulay *et al.*, 2016).

Collective foraging decisions are experimentally best revealed in binary choice experiments where groups of animals are presented two equidistant and identical food resources. If resource patches are not limited in size, groups tend to distribute asymmetrically between patches, showing the influence of social interactions on individual choices (Beckers *et al.*, 1990). Although research on collective foraging has initially focused on how groups find the shortest path to a food source or select the most energetic foods among many other alternatives, studies increasingly investigate the influence of food nutrient content and the diversity of nutritional needs between group members on collective behaviour and their evolution (Csata *et al.*, 2020).

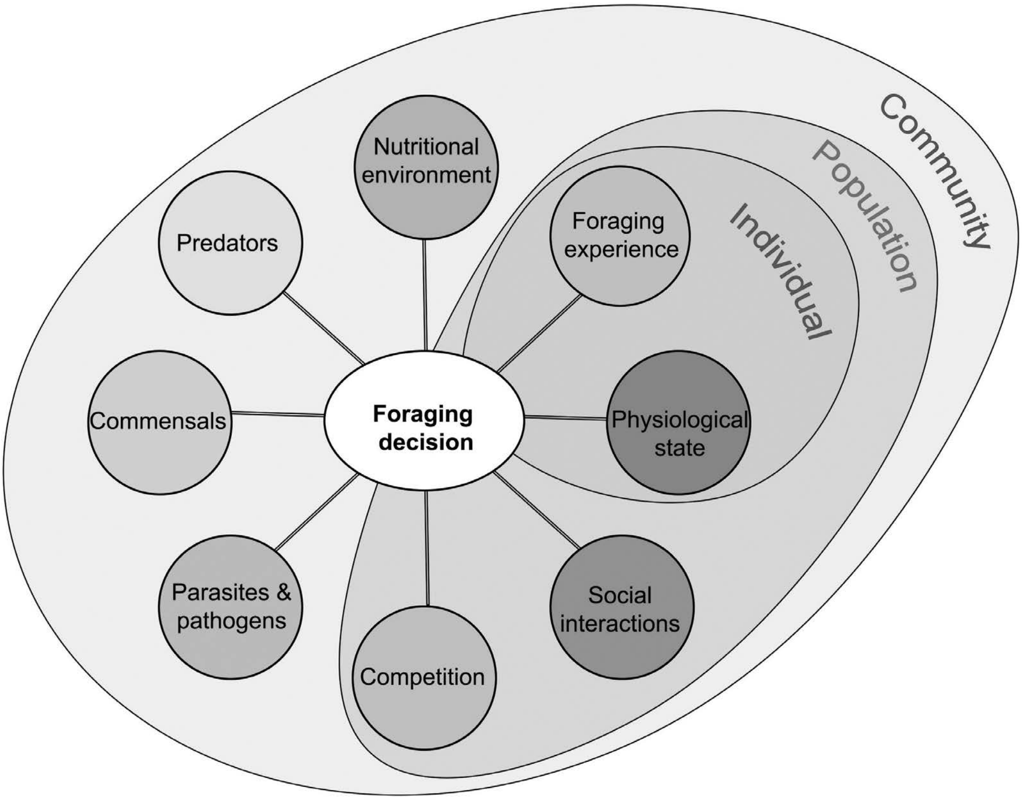

Figure 10.2 The multi-dimensional aspect of foraging behaviour. An animal's foraging decision results from interactions between multiple factors at the individual, collective and community levels.

Towards an integrative study of foraging behaviour

Above we have seen that many factors can affect an animal's foraging decision. A major challenge for foraging research is therefore to develop a more integrative, multi-level approach to the study of these behaviours. This involves considering the independent and interacting influences of the internal state of the animal (e.g. foraging experience, physiological state), the social environment (e.g. social interactions, competitive interactions), but also the broader ecological environment (e.g. available nutrients, predators, commensals, parasites and pathogens) on foraging decisions (Figure 10.2). Theoretical models have begun to explore what such integration may look like (e.g. (Lihoreau *et al.* (2017)). Below we illustrate how experimental research can be developed, using recent studies on pollinators exploiting floral resources.

Bees, butterflies, hummingbirds, bats and many other nectar feeders face the challenge of foraging on patchily distributed flowers. As such, they have been key models for the development of OFT (Pyke, 1984), collective animal behaviour (Seeley, Camazine and Sneyd, 1991), and are increasingly used in nutrition studies (Wright, Nicolson and Shafir, 2018). Social bees, in particular, provide many advantages for integrating studies on the spatial, nutritional and social dimensions of foraging. For a bee, foraging is a complex spatial problem that can involve visiting hundreds of flowers, sometimes distributed over several square kilometres, from a central nest (von Frisch, 1967). Flower resources regularly replenish over time (e.g. a flower produces new nectar, a tree produces new flowers) so that bees can learn to exploit most productive feeding sites through repeated foraging events. Foraging on flowers is also a complex nutritional problem. Bees must collect diverse food resources (nectars and pollens) that can greatly vary in their nutrient contents as well as their total energy. Individual foragers must obtain specific amounts and ratios of these nutrients to address their own nutritional needs as well as that of all other colony members, which includes the non-foraging workers that require carbohydrates as a source of energy, and the queens and the larvae that primarily need protein for growth and reproduction. Finally, in social species, such as honey bees and bumblebees, foraging is a collective task in which social and competitive interactions are central for the coordination and efficient collective action of foragers. Understanding how bees move, choose plant resources, and interact is a fundamental theme in modern foraging research. It is also of interest for comparative psychology and cognitive ecology as many animals exploiting scattered food resources must solve similar foraging problems but with very different brain sizes, architectures and computation power. Beyond behavioural sciences, addressing these questions also holds considerable promise for understanding the mechanisms ruling a major ecosystem service: pollination.

Integrating movements and cognition

It has long been assumed that bees use rules of thumb to move between food resources, for instance by flying between nearest neighbour flowers, keeping constant arrival and departure directions between visiting flowers, or moving up in an inflorescence (Pyke, 1978). While this may be true at small spatial scales, within a patch of flowers, bees appear to heavily rely on spatial learning and memory at larger spatial scales, when moving between patches of flowers (Lihoreau et al., 2012).

Early field observations suggested that bees foraging on multiple feeding locations learned stable foraging sequences to always revisit known locations in the same order, even if this led to very inefficient routes. This type of behaviour is referred to as “trapline foraging” (Thomson, Slatkin and Thomson, 1997). Experiments using arrays of artificial flowers (i.e. feeders containing sucrose solution as surrogate of nectar) to manipulate the quality and location of feeding sites through time, show that bees do not develop these routes by moving randomly or by visiting flowers in the order they first discovered them. Remarkably, as expected from an OFT approach, bees tend to find the shortest possible route to visit as many flowers as is necessary to fill their nectar crop (stomach) and return to their nest (Ohashi and Thomson, 2009; Buatois and Lihoreau, 2016). This optimisation behaviour is akin to solving the well-known Traveling Salesman Problem in mathematics for which there is no simple solution.

The process of route optimisation was described in details using a harmonic radar to record the flight trajectories of bumblebees carrying a transponder while developing a route in the field. Under these conditions, individual bees consistently found the shortest possible route by linking pairs of flowers using straight lines (vector flights), thereby optimising overall travel distances (Lihoreau *et al.*, 2012). Presumably, bees learn vector flights to link targets and selectively reuse those vectors that constitute the most economic routes so far experienced by the bee. While bees can develop and stabilise traplines within a few hours, they also occasionally test new routes and explore unfamiliar areas during the learning process (Woodgate *et al.*, 2017). Displacing artificial flowers after a bee has established a trapline, shows how foragers can rapidly find and integrate newly discovered flowers into a new optimal route (Lihoreau *et al.*, 2012). Continuous sampling may provide a powerful strategy to keep track of the quality of available resources and adjust foraging decisions to environmental changes, for instance if a resource becomes depleted.

Integrating nutrition

Not only do bees attempt to optimise travel distances when deciding which flowers to visit and in which order, they also choose flowers based on the volume or quality of nectar and pollen they contain. For instance, bumblebees foraging on artificial flowers delivering sucrose solution attempt to maximise their food collection rate (Lihoreau, Chittka and Raine, 2011). When all flowers are equally rewarding, bees visit them using the route minimising travel distances. However, when some flowers are more rewarding than others (which is the case in most natural conditions), bees' behavioural response varies depending on the location of the highly rewarding flowers. Foragers then trade-off between using a short detour from the shortest possible route to visit the most rewarding flower first and making no detour but with the risk that a competitor visits the most rewarding flower first.

Increasing evidence also show that bees selectively forage for particular nutrients in nectar and pollen. Studies with NG designs describe how isolated bees or small groups of bees given a choice between artificial nectars varying in their ratios of protein (or free amino acids) and carbohydrates regulate their acquisition of the two macronutrients to a specific intake target (Wright, Nicolson and Shafir, 2018). Bumblebees given a choice between pollens varying in their protein-to-lipids ratios also regulate their nutrient intake to target values (Vaudo *et al.*, 2016). In this process, lipid regulation appears critical (Ruedenauer *et al.*, 2020), especially in the presence of larvae in the colony (Kraus *et al.*, 2019). Honey bee colonies were observed to be capable of choosing foods in order to compensate for a single missing nutrient (e.g. amino acid) in their diet (Hendriksma and Shafir, 2016). This is a critical behaviour as the inability to do so can reduce the cognitive performances of foragers, ultimately threatening colony nutrition and development (Arien *et al.*, 2015).

Integrating socio-competitive interactions

In their natural environment, bees often exploit resources that are also available to other nectar foragers from the same colony, different colonies, or different species. Few studies have investigated the foraging patterns of competing pollinators in the field because it is technically challenging to track several flying insects interacting over large spatial and temporal scales. However, experiments in simplified environments, using artificial flowers, have revealed the importance of social and competitive interactions in bee movements and flower choices.

At the most basic level, bees can use information provided by other foragers to quickly assess the location and quality of beneficial resources. Honey bees, for instance, famously rely on an active symbolic communication, the "waggle dance", to recruit conspecifics to high quality feeding sites (von Frisch, 1967). The resulting mass foraging displayed by colonies is particularly beneficial in environments where resource patches are large but ephemeral and difficult to locate (Dornhaus and Chittka, 1999). For bees that exploit smaller resource patches, social information about resource quality can be gleaned through scent marks passively deposited by foragers during flower visits (Stout, Goulson and Allen, 1998) or visual observation (Worden and Papaj, 2005). In this way, inexperienced bumblebees during their first foraging trips can acquire preferences for flower colours and shapes (Worden and Papaj, 2005), or learn foraging techniques (e.g. pushing a ball in a hole (Loukola *et al.*, 2017)). Observational learning can also occur between individuals of different species (Dawson and Chittka, 2012) as many pollinators are generalists and benefit from a broad range of information about plant resources. Interestingly, bees seem to adjust their utilisation of social information depending on competition pressure, for instance by following social cues if they predict a reward (low competition) and avoiding them if they are associated to an absence of reward (intense competition) (Dunlap *et al.*, 2016).

These individual foraging decisions can considerably influence spatio-temporal patterns of social interactions within populations. As expected from OFT models of ideal free distribution (Fretwell and Lucas, 1970), bees foraging in a common area tend to self-distribute themselves in a way that minimises competition and maximises individual foraging efficiencies (Dreisig, 1995). When resources are patchily distributed, this means that individual foragers should specialise on different foraging areas. Experiments with populations of bumblebees in outdoor flight tents confirm that foragers learn to avoid extensive spatial overlaps with conspecifics. Spatial partitioning emerges from basic rules of competition by exploitation (i.e. resources exploited by competitors are found empty) and competition by interference (i.e. competitors physically interact for accessing resources) (Pasquaretta *et al.*, 2019). In this process, more experienced foragers indirectly deter competitors by increasing their frequency of visits to familiar flowers, so that newcomers find these flowers empty and look for other opportunities. Occasionally, these more experienced bees also tend to land on familiar flowers occupied by competitors and displace them through physical interactions, gradually leading to space partitioning between foraging bees.

Integrating environmental stressors

Many environmental factors, other than plant spatial distribution, nectar and pollen nutritional contents, and the presence of competitors, affect the movement patterns and foraging decisions of bees. Specifically, flowers can be associated with the presence of predators, parasites and pathogens that bees should attempt to avoid in order to minimise fitness losses.

When sitting on flowers, bees risk being attacked by predators, as for instance crab spiders that can change colour to match flower's visual aspect. Experiments using robotic crab spiders to control for predation risks showed that bumblebees can learn to associate the colour of a flower to the presence of spiders, ultimately reducing visits to other flowers of the same type even if they have no spider (Ings and Chittka, 2008). Reducing the conspicuousness of spiders by rendering them more similar to the colour of the flowers showed how bees can increase flower inspection times to avoid being injured or eaten.

Flower nectar and pollen contain many parasites, such as trypanosomes and microsporidia and bees can avoid visiting these contaminated flowers (Graystock *et al.*, 2020). For instance, bumblebees given a choice between sucrose solution containing a gut parasite specific to bumblebees (*Crithidia bombi*) and sucrose solution free of parasite were found to prefer feeding on the non-contaminated solution, whereas no discrimination was observed when a non-specific pathogen (*Escherichia coli*) was added to sucrose solution (Fouks and Lattorf, 2011). In some cases, bees may also forage on plants with pollens, nectars or resins containing substances useful to avoid diseases or as a mean for medication once infected by parasites or pathogens (Spivak, Goblirsch and Simone-Finstrom, 2019). Bumblebees use nicotine in nectar to combat gut parasites (Baracchi, Brown and Chittka, 2015). Model simulations implementing such selective foraging behaviour show that collective regulation of prophylactic and curative substances by bee foragers, based on NG principles, can be a powerful way to slow down and limit infections in colonies (Poissonnier *et al.*, 2017).

Agrochemicals constitute another essential source of environmental stress that can profoundly affect bee foraging behaviour. Bees increase the yields of human crops, but in doing so, are inadvertently exposed to pesticides in floral nectar and pollen. Neonicotinoids used in seed coating to control herbivorous insect pets in a variety of crops, have attracted much attention over the past years. For instance, honey bees and bumblebees exposed to sub-lethal doses of these pesticides in food have difficulty to learn floral traits, feed, navigate, and forage (Henry *et al.*, 2012). It is concerning that bees cannot detect field realistic concentrations of these neonicotinoids in food. Even worse, foragers show a preference for solutions containing neonicotinoids over sucrose alone, even if consuming these solutions is likely to kill them (Kessler *et al.*, 2015). This preference for laced solutions is probably due to the pharmacological action of neonicotinoids on nicotinic acetylcholine receptors in the bees' brains, so that insects associate the neuroactive effect of the pesticide to the solution.

Preserving an ecosystem service

Beyond advancing fundamental knowledge on animal behaviour, developing a more integrative research program on foraging behaviour can also illuminate broader ecological processes resulting from interactions between foraging animals and their environment. In the case of bees, understanding how individuals forage on plant resources can bring insights into the mechanisms of pollination.

When moving between flowers, bees transfer pollen grains and mediate the reproduction of plants. Current models attempting to predict these interactions in space and time assume that bees move randomly or use simple rules of thumb, so that pollen dispersal follows homogenous patterns in every direction (isometric diffusion) within the foraging range of bees (e.g. (Vallaeys *et al.*, 2017)). This assumption certainly suffices to describe broad patterns of plant crossing and genetic isolation by distance (Wright, 1943). However, at a finer spatial scale, considering the complex, multidimensional aspects of bee foraging behaviour can change predictions about pollination. Specifically, the non-random foraging movements of bees between distant plants may generate non-random pollen dispersal and plant mating patterns that can critically and predictably influence plant fitness (Ohashi and Thomson, 2009). For instance, it can be predicted that the average mating distance between plants (a measure often linked with plant fitness) differs drastically if bees are assumed to visit plants randomly (Figure 10.3A) or if they learn traplines minimising travel distances (Figure 10.3B). Different bee species exhibiting different spatial strategies may have different impacts on pollination. It can be argued that mass foraging bees, such as honey bees that recruit nestmates to feeding sites, may favour low mating distances and high rates of self-pollination as a result of many bees revisiting the same flowers. Such collective foraging behaviour may lead to relatively poor-quality pollination and low reproductive success of plants due to self-incompatibility or inbreeding depression. By contrast, solo foraging bees, such as many solitary bees and bumblebees, that do not recruit conspecifics to specific sites and instead develop non-overlapping traplines, may produce increased pollen dispersal

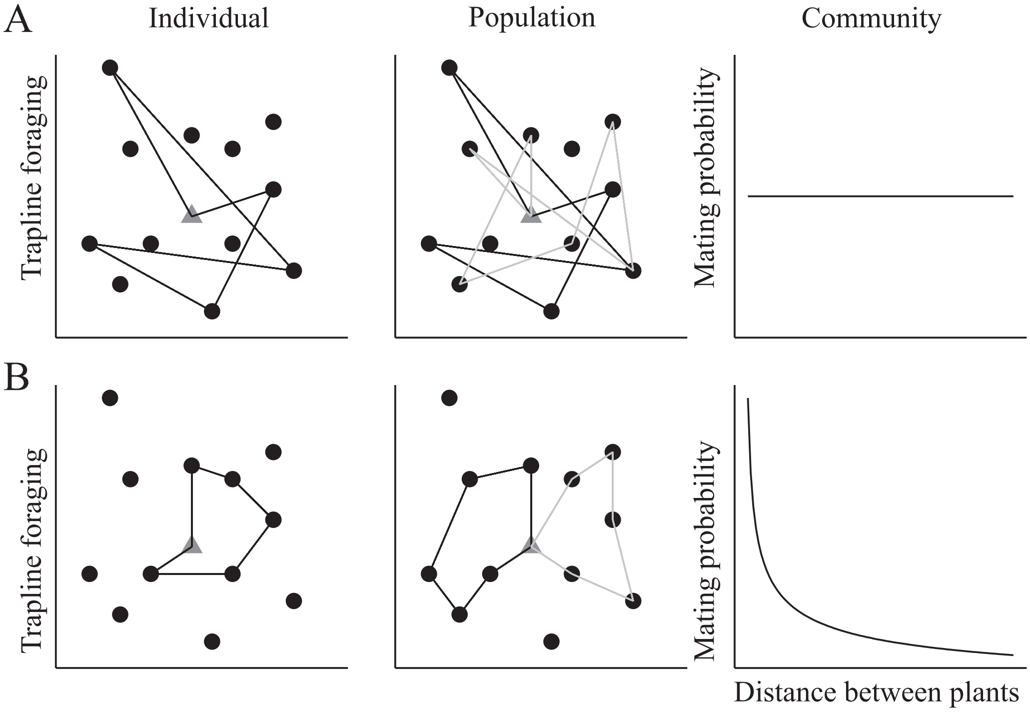

Figure 10.3 The impact of bee foraging movements on pollination. Hypothetical examples of bee foraging patterns (lines) between plant resources (dots) and their nest (triangle), and their expected impact on mating patterns (graphs). Different descriptions of behaviour at the individual level lead to different predictions at the population levels and community levels. A. Bees are assumed to move randomly between plants: competing bees (black and grey lines) occasionally visit the same plants, and plant mating is independent of the distance between plants. B. Bees are assumed to learn plant locations and develop traplines to link them efficiently: competing bees tend to avoid exploiting the same plants, thus favouring crossings between plants that are located within the same area.

and higher frequencies of out-crossings. Future experiments to unravel these behaviours and their consequences on plant mating patterns will clarify the mechanisms by which different species of pollinators may complement each other for plant reproduction (Garibaldi, 2016). These findings may guide the design of practical interventions regarding how managed bees can be used to improve food production through alternative practices to agrochemicals. They could also help identify environmental conditions favouring wild communities of plants and pollinators in the context of pollinator declines (Goulson *et al.*, 2015)

Concluding remarks

Foraging encompasses a suite of behavioural decisions that can be studied independently from each other using concepts and methods from the different fields of behavioural research. However, recent attempts to integrate these different approaches in model species such as bees show the considerable gain that can be made to understand the behaviour of individuals, but also their interactions within populations and the ecological environment. Studying these interactions across levels of biological organisation holds considerable promise for tackling general questions about species co-existence, community structures and ecosystem services (see examples in Box 10.1).

Box 10.1

Examples of fundamental questions in ecology and evolution that would benefit from a more integrative understanding of animal foraging behaviour.

1) It has often been argued that constraints related to food access are major evolutionary drivers of social life (Lihoreau *et al.*, 2017). Can we identify specific nutritional pressures (e.g. lack of specific nutrients in foods, need for collective exploitation of food items) that led to the evolution of different forms of animal societies?
2) Many parasites can be found in the form of spores in food (Graystock et al., 2020). When foods are exploited by multiple animals, to what extent can understanding patterns of foraging interactions between these animals predict parasite transmission, dynamics and evolution?
3) Social insects regulate colony nutrient intake through the collective action of workers (Csata et al., 2020). How do other group-living animals, in general, solve nutritional conflicts when different individuals in a group have different nutritional needs, for instance when parents feed their juveniles?
4) There have been attempts to seed flowering plants in urban and agriculturalhabitats to provide food for wild pollinators (Goulson et al., 2015). To what extent can we manipulate the availability, spatial distribution and nutritional quality of food resources for animal conservation?
5) Knowing how bees move and interact between plants provides key insights about plant mating patterns (Ohashi and Thomson, 2009). To what extent can we manipulate pollinator foraging movements to improve essential pollination services?

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11

CAUSAL FACTORS IN THE STUDY OF VIGILANCE

Guy Beauchamp

Introduction

Threats shape many aspects of the lives of animals. Living in habitats with low predation risk, for instance, can affect the size of mammalian and avian groups (Blumstein and Daniel, 2005) and even morphological features such as coloration in fish and tail length in tadpoles (Relyea, 2004). Animals can reduce risk through several means including morphological and behavioural adaptations (Caro, 2005). For example, some behavioural adaptations, like spatial aggregation, reduce the rate of encounter with predators. Others, like vigilance, increase the likelihood that threats are detected before it is too late to escape. Yet other adaptations, including group defence and escape movements, increase the chances of evading actively pursuing attackers. In this chapter, I focus on vigilance.

Vigilance relates to the state or the action of keeping careful watch for potential danger. In the ecological literature, vigilance involves monitoring threats caused by predators (antipredator vigilance) or conspecifics (social vigilance) (Beauchamp, 2015). In the psychological literature, the label 'risk assessment' describes behavioural patterns associated with the detection of threats or the increased alertness that follows detection (Blanchard et al., 2011). Without the ability to detect neural signatures associated with risk assessment, external markers of vigilance, such as head movements, are the only direct way of measuring vigilance.

Vigilance can be pre-emptive or reactive. With pre-emptive vigilance, animals aim to detect signs of danger before an attack occurs. Reactive vigilance relates to the actual monitoring of threats after detection. Reactive vigilance allows animals the time necessary to assess the level of threat caused by a predator or a conspecific and to choose between fleeing and fighting. Some researchers associate fear responses with imminent threats, which would be the domain of reactive vigilance. Pre-emptive vigilance might be associated with anxiety as the threat is not imminent (Bouton et al., 2001). Psychologists echo the distinction between pre-emptive and reactive vigilance as they distinguish between potential and proximal threats (Mobbs et al., 2015).

The social environment of an animal is a key factor influencing vigilance. Opportunities for conflicts or competition in general increase with group size. In this case, social vigilance, which is aimed at competitors, is expected to increase in larger groups (Treves, 1999). Antipredator vigilance, by contrast, is expected to decrease in larger groups through several mechanisms. In a group, the presence of more eyes and ears attuned to risk detection enables group members to relax their vigilance at no increased risk to themselves (Pulliam, 1973; Roberts, 1996). To benefit from this collective vigilance, individuals that have failed to detect a threat on their own must be able to react rapidly to the signs of alarm provided by companions (Lima, 1995). Such signals include alarm calls or indirect

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cues of alarm like noises associated with flight (Hingee and Magrath, 2009) or feeding interruptions (Pereira et al., 2012). Facial expressions of fear can also work as alarm signals and might be recognized by some animals (Tate et al., 2006). Another important consideration is that the risk of capture of any group member is diluted by the presence of more targets for the predator (Bertram, 1978). Better detection and risk dilution can on their own or together allow a reduction in antipredator vigilance as group size increases (Roberts, 1996).

In the ecological literature on vigilance, the bulk of the research has focused on the adaptive value of vigilance, namely, how vigilance allows individuals to increase their survival. Ecologists have neglected other questions that apply to all behavioural patterns including development, causality, and evolution. In the psychological literature, the emphasis has been on studying causality, including the neural basis of responses to threats (Mobbs et al., 2015) – especially in humans.

In this chapter, I aim to highlight causal factors relevant to the study of vigilance. Several causal factors can play a role in producing vigilance. Threats are perceived and then assessed to produce a response like freezing or fleeing. Causal factors in vigilance can be involved at the perceptual stage and during processing in higher brain centres. More details can be found in recent reviews (Blumstein, 2020; Beauchamp, 2017). For ecologically minded researchers, this chapter might be useful by emphasizing findings from a less familiar literature. The chapter also presents data from the field, which might allow more psychologically minded researchers to think more broadly about the study of risk assessment.

Causal factors in vigilance

Hormones

Hormones can affect the internal state of an individual thus modulating the expression of vigilance. Hormones that control the sleep-wake cycle are involved in vigilance by allowing individuals to respond to external threat stimuli (Dijk and Lockley, 2002). Being awake is a necessary condition for vigilance, but it is generally not sufficient to modulate vigilance.

Testosterone and oxytocin are two hormones that modulate vigilance more finely. In some species, males are more vigilant than females, suggesting that sex hormones might be involved. Treated with testosterone, male grey partridge (*Perdix perdix*), for instance, maintained a higher vigilance than non-treated males both before and after the presentation of a threat (Fusani et al., 1997). Some research suggests that testosterone affects how persistently individuals search for specific stimuli (Andrew, 1978), which might be useful when individuals are on the lookout for potential competitors. In humans, testosterone was linked to increased attention to threat signals (van Honk et al., 1999), again suggesting a role during social vigilance. Testosterone might thus influence vigilance by increasing monitoring effort. As secretion of testosterone often fluctuates over the annual cycle, vigilance levels might show parallel variation. Whether testosterone affects the expression of antipredator vigilance is not clear.

Like testosterone, oxytocin appears to modulate social vigilance. Monkeys that received an exogenous dose of oxytocin showed increased attention to the eyes of companions (Ebitz et al., 2013). The most remarkable finding was that oxytocin reduced social vigilance, which would favour prosocial behaviour (Chang and Platt, 2014). The association might also work in the opposite direction: if prosocial behaviour increases the secretion of oxytocin, it might lead to a reduction in social vigilance. The secretion of oxytocin involves brain structures such as the amygdala, which in primates regulates attention and arousal to facial features involved in the modulation of social vigilance (Gothard et al., 2007).

Faced with danger, animals should be able to focus on the threatening stimuli and ignore non-crucial, rival sources of attention. The stress response in vertebrates is designed to do just that. The stress response involves a series of short- and long-term physiological changes that enable animals to mount an effective defence against a potential threat (Charmandari et al., 2004). Well-known consequences of the stress response include an increase in heart rate and a sharpening of the senses. Darwin long ago suggested that emotions such as fear facilitate the perception of danger allowing a better response to threats (Darwin, 1872). In particular, he noted that fear induces remarkable changes in facial expression including widening of the eyes and distention of the nostrils. A study in humans mimicking different facial expressions showed that when expressing fear, individuals could see more widely, move their eyes faster during a targeting task, and inspire more air when breathing (Susskind et al., 2008). All these changes induced by the stress response would increase visual and olfactory perception of threats and thus influence the quality of vigilance. As a good example, secretion of norepinephrine during the stress response can increase pupil size (Eldar et al., 2013). While an increase in pupil size typically decreases visual acuity, it also allows individuals to focus on movement and high contrast features of the eliciting stimuli thus tuning out less relevant features. In monkeys, presentation of socially relevant stimuli increased pupil size as expected (Ebitz et al., 2014). In peacocks (*Pavo cristatus*), pupil size increased after the presentation of a predator model (Yorzinski and Platt, 2014). Such changes in pupil size might thus be considered an external marker of the state of vigilance.

Hormones like corticosteroids are also released following an acute stressor such as exposure to predators (Harris and Carr, 2016). One study found that circulating cortisol (a corticosteroid) decreased in sheep (*Ovis aries*) living in larger groups (Michelena et al., 2012), which was expected as predation risk, an acute stressor, decreases as group size increases. The level of vigilance in this species also decreased with group size although it is not clear whether the decrease in vigilance allowed the reduction in cortisol or vice versa. Other field studies also assessed the relationship between vigilance and corticosteroid production. Fecal corticosteroids (including cortisol) collected opportunistically in the field showed no relationship with vigilance levels in olive baboons (*Papio anubis*) (Tkaczynski et al., 2014) but increased in more vigilant meerkats (*Suricata suricatta*) (Voellmy et al., 2014). In Yellowstone, elk (*Cervus elaphus*) vigilance increased in areas with higher predation risk (Liley and Creel, 2008). However, fecal glucocorticoids failed to match vigilance levels (Creel et al., 2009), which raises the possibility that predation risk can influence vigilance without involving the release of corticosteroids.

To elucidate cause and effect in the vigilance response, some studies have used exogenous sources of corticosteroids to examine consequences for vigilance but with limited success (Santema et al., 2013; Voellmy et al., 2014). Thus far, therefore, the association between corticosteroid production and vigilance appears weak. Some studies suggest that corticosteroids might play a role in attentiveness to external stimuli and the consolidation of memory (Mateo, 2014). Rather than controlling the total amount of time allocated to vigilance, corticosteroid secretion might instead play a role in the *quality* of vigilance.

Brain areas associated with vigilance

The release of hormones depends ultimately on activation in specific brain areas. Brain structures can thus have an indirect role in vigilance by affecting hormone production. However, studies detailed below suggest that specific brain areas can also play a more direct role.

Ethologists have long established that certain stimuli can capture an individual's attention more easily (Tinbergen, 1951). Targeted attention during vigilance could also allow individuals to detect potential threats more quickly. Neural circuits underlying targeted attention have been identified in the brains of mammals (Pellman and Kim, 2016). Aggression in primates, for instance, involves gaze and body direction as well as facial expressions. Specialized neural cells that specifically respond to such stimuli have been discovered in the brains of primates (Emery, 2000). Many specialized neural cells associated with vigilance occur in the superior temporal sulcus (STS) and the amygdala. Physiological experiments have revealed that in monkeys the STS responds to the eyes and the orientation of the head and body. The amygdala is involved in attaching a socio-emotional significance to these signals (Emery, 2000). For example, staring by a companion would recruit the STS, and the amygdala would in turn recognize that such staring represents a sign of dominance for which an appropriate response might be vigilance.

The amygdala modulates fear and anxiety in humans (Sander et al., 2003). Following the perception of a threat, the amygdala activates psychophysiological reactions and emotions such as vigilance. In primates, lesions to the amygdala lead to impaired judgement about facial features, which are crucial to decode aggression. In short, the amygdala monitors the environment for potentially threatening signals (Whalen, 1998). Whether the amygdala or similar brain structures play a role in vigilance in species other than primates is not yet clear.

Specific abilities to produce vigilance

In this section, I examine specific causal processes involved in vigilance. These causal processes are based on specific abilities needed to produce vigilance responses.

Vigilance and estimation of group size

Many studies in birds and mammals have documented a decrease in vigilance with group size (Elgar, 1989). Could this ability be one example of numerical competence in the wild? Sensitivity to the number of things is defined as numerical competence (Gallistel, 1993). Numerical competence includes a continuum of abilities ranging from discrimination among sets of things according to the number of items (discrimination of the less-versus-more type), to counting the number of things in a set (having an absolute enumeration of a particular discrete number), and performing arithmetic. Many species of animals can discriminate numbers of stimuli and also appear to have a concept of number (Nieder, 2020).

A wide range of species from salamanders to monkeys can discriminate between different quantities after extensive training. However, there are few examples of spontaneous, unprompted numerical abilities in the wild. Studies of territorial disputes between rival groups suggest the ability to adjust behaviour to the number of opponents (Radford and Du Plessis, 2004; McComb et al., 1994), but this assessment might rely on indirect cues such as the amount of noise produced by the contestants. The ability to count has also been invoked in one bird species in which the number of eggs produced at a given time depends on the number of eggs already present discounting those laid parasitically by conspecifics (Lyon, 2003). Movement decisions in wild olive baboons also appear to involve numerical estimation (Piantadosi and Cantlon, 2017). Nevertheless, some researchers claim that wild animals are unlikely to confront situations that select for elaborate numerical competence such as true counting (Hauser, 2000).

The fact that behaviour varies with group size need not imply that individuals use counting. For instance, in many species aggression typically increases with group size. Rather than being based on counting, aggression might be simply dependent on the rate of encounter between foragers. Forager density (the number of animals per unit space) often tends to be correlated with group size (Battley et al., 2003). An increase in the rate of encounter with companions could thus indicate a larger group. Recent work with fruit flies (*Drosophila melanogaster*) suggests that both group size and density can independently influence behaviour in groups and that social networking, for instance, depend more on group size than density (Rooke et al., 2020).

Other types of cues can be used to adjust behaviour to group size. Individuals produce visual and non-visual cues that are not enumerable. For instance, individuals can produce scents, make noise or occupy a certain area in space. Overall production of scent or level of noise in a group and/or the area occupied by the group may reflect group size. All these cues could be estimated on a qualitative scale (e.g. less or more). In territorial disputes, animals have been shown to adjust their attack strategies to the amount of noise produced by rivals (Radford and Du Plessis, 2004; McComb et al., 1994). In fruit flies, the ability to detect male pheromones is important to adjust behaviour to group size (Rooke et al., 2020), suggesting a response to scents produced by other group members. Humans appear to be sensitive to visual non-enumerable cues such as area and contour length of sets of attributes (Hurewitz et al., 2006). When group size increases, the area occupied by the group as well as contour length necessarily get larger. Therefore, a response to group size might indicate a response to area and contour length rather than number *per se*.

One way to address the issue of non-enumerable cues in the context of vigilance would be to use video images of companions. Studies have shown that animals respond to video images of companions as they would to live animals (D'Eath, 1998). Videos with more foragers can also induce a decrease in vigilance (Rieucau and Giraldeau, 2009). A barrier could prevent the use of scents and sounds produced by companions. By varying the position of video companions, sideways versus frontal for instance, and the space that they occupy on the monitor, it should be possible to create video displays of groups of different sizes while maintaining area and contour length the same. If individuals really count they should respond to the number of foragers in their visual fields rather than to the space they occupy or the contour length.

Some might argue that the ability to count in order to adjust vigilance to variation in group size is expecting too much from wild animals. Involving an ability to count or to accurately represent small differences in group size can actually be more parsimonious than more reductionist explanations based on less elaborate abilities (Bekoff, 1998). For example, non-cognitive rule-of-thumb explanations did not account for the flexibility in vigilance behaviour shown by one bird species in response to changes in group geometry as well or as simply as explanations that appealed to the cognitive capacities of the birds (Bekoff, 1996). Some of the indirect mechanisms described earlier to estimate group size also involve cognitive skills (e.g. estimating the rate of encounter with neighbours). An appeal to elaborate numerical competence is simple and no more complex than some of the alternative explanations and could have wide explanatory power.

Vigilance and scalar timing

Different types of predators require different types of adjustments to vigilance. Stalking predators like cats that approach their prey surreptitiously could take advantage of any regularity in prey vigilance to advance closer. Prey that face stalking predators should thus initiate their vigilance bouts at unpredictable times (Scannell et al., 2001). Unlike cats, avian raptors rely on surprise attacks to approach their prey. Facing such predators, prey should initiate their bouts of vigilance at fixed rather than unpredictable times (Bednekoff and Lima, 2002).

Intervals between vigilance bouts are known as interscan intervals. In contrast to regular vigilance, unpredictable vigilance should lead to much variability in the duration of interscan intervals. Surprisingly, empirical distributions of interscan interval durations show substantial variability even when prey face non-stalking predators (Pays et al., 2010). This is perplexing because shorter intervals than expected are unlikely to be informative if non-stalking predators are rare and longer intervals than expected could allow predators to get closer. External disturbances unrelated to predators (such as random noises) might cause this large, unexpected variability by forcing vigilance to occur at times others than those expected (Ruxton and Roberts, 1999). Recently, I suggested that well-established cognitive processes associated with interval timing might be another factor responsible for variability in the duration of interscan intervals (Beauchamp, 2019).

Interval timing is ubiquitous in animals. Animals can use their internal clock to choose when to leave a patch for instance (Oprisan and Buhusi, 2014). In one influential model of interval timing, keeping time with an internal clock is considered inherently noisy because intervals between ticks are not constant (Gibbon et al., 1984). Another source of noisiness has also been identified when committing timing events to memory for subsequent retrieval. Such noise means that determining when time is up using the internal clock can produce different values from one timing event to the

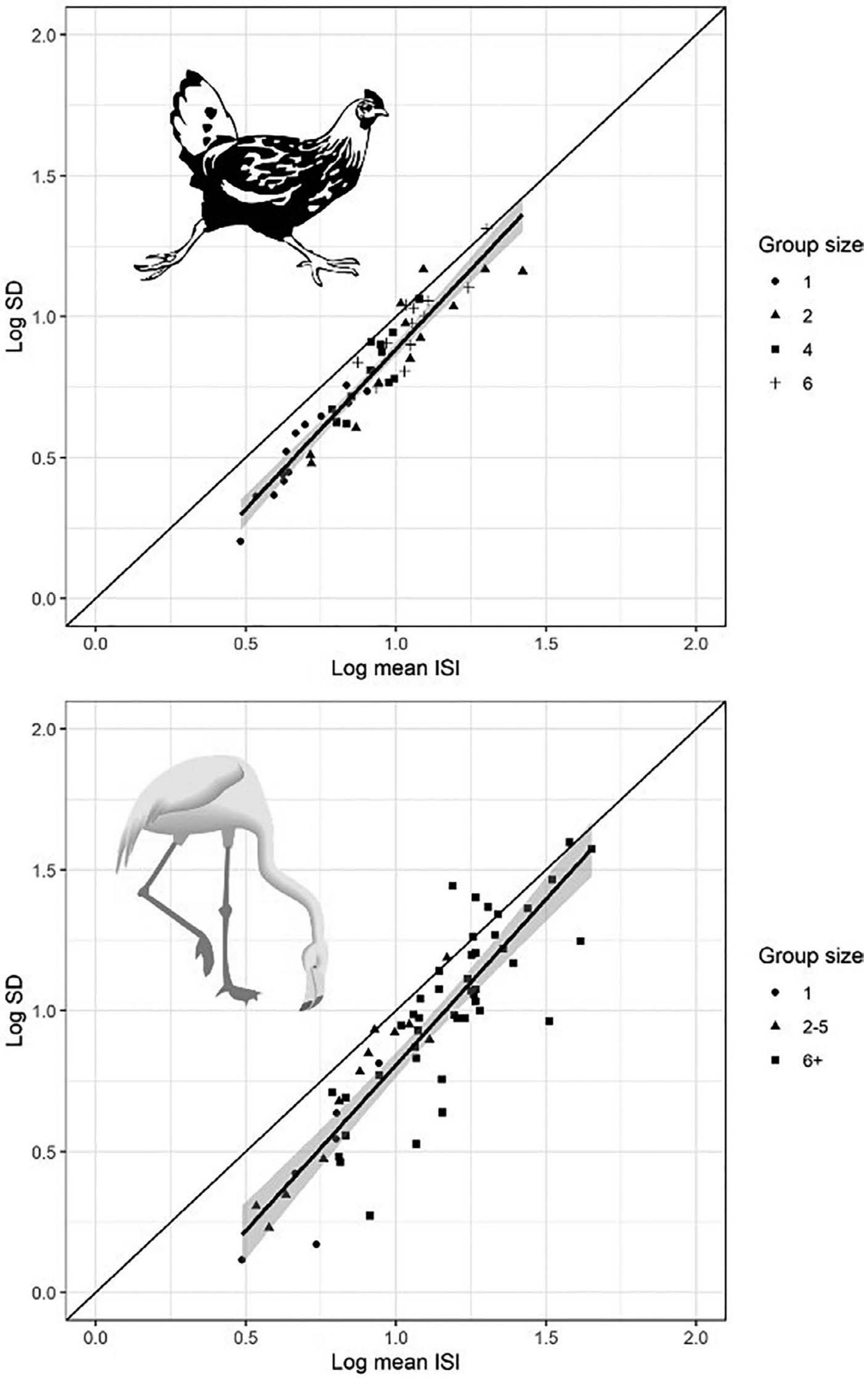

Figure 11.1 Association between the standard deviation (SD) of the duration of interscan intervals (ISIs) and the mean of these intervals in captive domestic fowls (top panel) and in wild American flamingos (lower panel) in groups of various sizes. Thick lines show a simple log-log regression line across the data to illustrate the fit of the model.

next. For example, an animal using the internal clock to initiate a vigilance bout after 10 s spent feeding head down will sometimes become vigilant before 10 s or after. The duration of an interscan interval could thus vary substantially from one bout to another due to noisy processes associated with interval timing.

How can we tell if noisy interval timing is involved? The noise (or error) around the expected interval duration should increase linearly with mean interval duration. Plotting the standard deviation of these intervals should show a strong, linear positive relationship with the mean duration of these intervals. Even more telling, the noise should be proportional to the mean interval duration implying that the coefficient of variation of these intervals should remain constant across the range of mean interval duration. These expectations follow from the scalar property of interval timing. Scalar timing should also lead to a right skew in the distribution of intervals rather than a normal distribution.

I tested these predictions in captive domestic fowls (*Gallus gallus*) and in wild American flamingos (*Phoenicopterus ruber*), two species of birds facing a wide range of predators including, but definitely not restricted to, stalking predators (Beauchamp, 2019). Due to the group-size effect on vigilance, the mean duration of interscan intervals is expected to increase with group size. This variation can be used to alter the expected mean duration of interscan intervals. In a plot of the variation in the duration of these intervals across a range of interval durations induced by changes in group sizes, I documented a strong positive relationship between the standard deviation and mean interscan interval duration (Figure 11.1). The empirical distribution of these intervals was also right-skewed, as predicted. However, the coefficient of variation of these intervals increased with the mean rather than remaining constant as predicted by scalar timing. Overall, interval timing accounted for some but not all features of the distribution of interscan interval durations. One possibility to explain why the coefficient of variation failed to remain constant is that group members influenced the timing of vigilance bouts, adding external noise on the duration of interscan intervals. These early results suggest that scalar timing could impose constraints on the timing of interscan interval durations, and further research is needed to assess the relevance of cognitive processes associated with interval timing to vigilance in animals.

Vigilance and laterality

In many vertebrates, information processing is divided between the two hemispheres of the brain (Rogers and Andrew, 2002). For species with eyes set laterally, particular tasks can thus be performed preferentially with the left or right eye, which would recruit the opposite hemisphere in the brain. Responses to predators and aggressive companions, for instance, tend to involve the left eye while the right eye is associated with foraging responses. Having a lateralized brain represents a convenient way to carry out two competing activities by allocating a different eye to each task. Chicks with lateralized brains thus performed better at a dual task that involved predator detection and concurrent food finding than those without lateralization (Rogers et al., 2004).

Whether animals prefer one eye to carry out vigilance has received some attention. Dark-eyed juncos (*Junco hyemalis*) tested under semi-natural conditions showed a preference to use the right eye for vigilance but not a closely related species (Franklin and Lima, 2001). Wild swan geese (*Anser cygnoides*) preferentially oriented the right eye toward danger although this was not the case for two other species sharing the same habitat (Randler, 2005). When semipalmated sandpipers (*Calidris pusilla*) used their right eye to monitor the area from which their main predators attack, they obtained more food than when they used their left eye (Beauchamp, 2013), suggesting that their right eye is better adapted at detecting potential predation threats. In one wild ungulate, a left-eye bias was evident when monitoring danger (Found, 2017).

The above results show little consistent preference for one eye versus the other during vigilance. Lack of a consistent preference might reflect the multi-faceted nature of vigilance. Vigilance involves different tasks, from monitoring the surroundings for signs of danger to the actual monitoring of an attacker. It could be the case that these different tasks are best suited to different brain hemispheres and thus to different eyes. To complicate matters, vigilance also reflects the need to monitor conspecifics, which might involve a different brain hemisphere. Studies that can tease apart the various kinds of vigilance are needed to ascertain the association between vigilance and laterality.

Conclusions

Research on the causal factors involved in vigilance helps us understand how animals produce vigilance. In this chapter, I covered various causal factors from hormones to specialized brain cells as well as cognitive processes involving counting and interval timing. Brain studies can be helpful to identify cognitive processes and areas that are involved in risk assessment. Nevertheless, such studies are limited in scope because they rely on a handful of species (very often only humans) studied in the laboratory under relatively artificial conditions. While studies in the wild involve more ecologically relevant conditions, causal factors are much harder to study in such environments. For instance, sampling live animals to measure hormones involves handling that can affect the very hormones under study. Nevertheless, some behavioural observations in the wild can provide us with information about cognitive processes such as laterality (through postures) or interval timing (through timing choices). I highlighted several new directions for research on causal factors in vigilance (Box 11.1). The recent call for collaboration between neuroscientists and ethologists is likely to further advances in this field in the coming years (Mobbs et al., 2018).

Box 11.1 Potential directions for future research on causal factors in vigilance

Can testosterone and oxytocin be involved in antipredator as well as social vigilance?

Is pupil size a good marker of vigilance across species and in different risk contexts?

In which contexts is a good or a poor match expected between levels of vigilance and corticosteroid production?

Does the amygdala or related structures play a role in vigilance in species other than primates?

Is the adjustment of vigilance to group size indicative of numerical competence or simply a response to non enumerable cues associated with group size?

Are cognitive processes associated with interval timing relevant in the distribution of interscan interval durations in animals?

Is there a preferred eye when scanning for predators or competitors?

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12

COMMUNICATION

Eleanor Caves, Patrick Green and Melissa Hughes

Most interactions between animals involve communication, and all communication shares fundamental features (Figure 12.1): a signaler produces a signal, which passes through the environment and is received by a receiver, eliciting a response. Signals allow receivers to assess information about the signaler or environment, and receiver responses impact both themselves and the signaler (see Table 12.1 for definitions).

This simple description belies considerable complexity in communication systems and the forces that influence their evolution (Figure 12.1B). The form, or physical structure, of the signal depends both

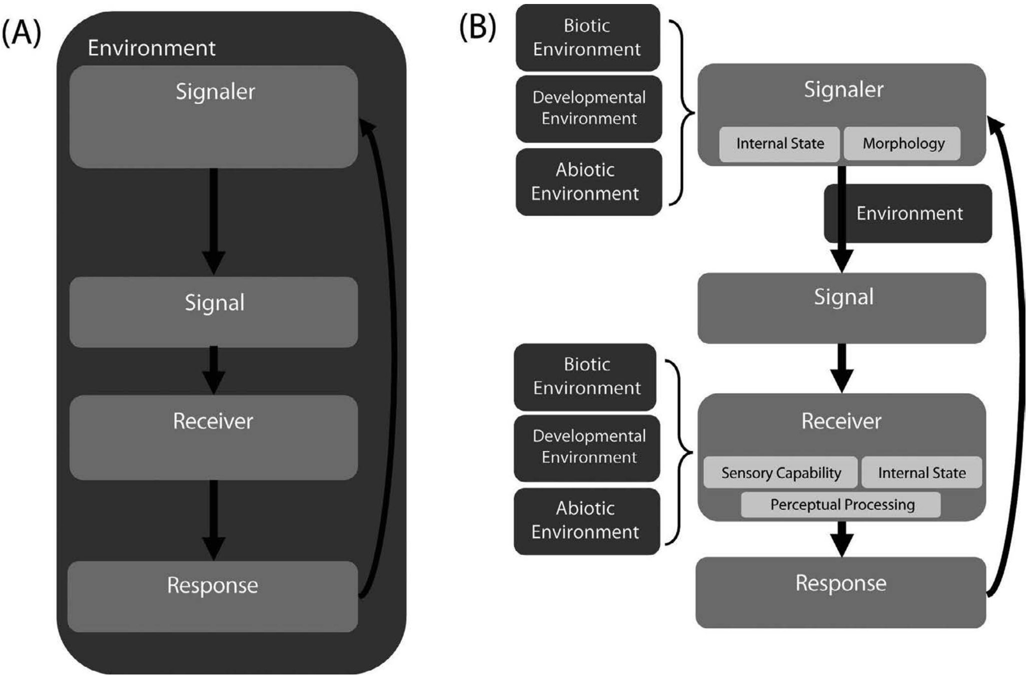

Figure 12.1 (A) Communication involves a signaler producing a signal that transmits through the environment and is received by a receiver, resulting in a response. (B) Each of these stages is influenced by a variety of other factors (see text for details).

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Table 12.1 Definitions (see also Searcy and Nowicki 2005)

Communication	behavioural exchange between two or more individuals, in which one individual ("receiver") obtains information from and responds to a signal produced by another individual ("signaler").
Signal	characteristic of or behaviour by the signaler that has evolved to change the behaviour of receivers; may also include structures made by signalers (Figure 12.2).
Information	measurable relationship between some signal characteristic and characteristic(s) of the signaler or environment.
Reliability or honesty	strength of correlation between a signal and information; receivers benefit when responding to reliable/honest signals.

on the signaler's ability to produce it and on the receiver's ability to detect it and discriminate it from other stimuli. Therefore, signal evolution is bounded by selection on the signaler's morphology and/or physiology, and on the receiver's sensory and cognitive systems. In addition, the environment may filter or otherwise modify the signal's characteristics during transmission, affecting how it is perceived by receivers. Because of this, environmental properties are an additional selective pressure on the behaviour and/or physiology of both signaler and receiver. Finally, the interests of the signaler and receiver in the outcome of the interaction may be the same, or they may differ. In the latter case, selection on signaling systems may occur under conflicting selection on the two individuals involved.

In this chapter, we'll take a closer look at each of these factors separately, while noting interactions between them. In Section I, we'll explore axes of diversity and complexity in signal characteristics, and consider how signal form may relate to signal function. In Section II, we'll discuss signal transmission, and in Section III, we'll explore the role of receiver sensory systems and cognitive processing in shaping signal evolution. Section IV will expand the discussion beyond the production of and response to a single signal.

I. Signals and signalers

Studies of animal communication typically begin with the signal: for example, a song, a claw-wave, elaborate tail feathers. But what exactly about a signal is relevant to receivers? Consider a color patch – could the relevant characteristic be the patch's size or shape, its hue or brightness, its contrast with neighboring color patches, or how one of these variables changes through time? What signal characteristic allows receivers to assess information about the signaler or environment? Signals function to change the receiver's behaviour (see Table 12.1), but the diversity of signal forms that achieve this function seems endless (Figure 12.2). Below, we highlight some of the diversity and complexity in signal forms and their relationships to signal function; Box 12.1 provides an exploration of these issues in a single, relatively simple, signal.

Signal diversity & complexity

One common way to classify a signal is by the main sensory modality with which it is perceived (visual, acoustic, chemical, tactile, electrical, etc.). Indeed, much work on animal signals focuses on those perceived by a single modality. Nonetheless, many signals are "multimodal": individual signals simultaneously perceived in more than one modality (e.g., movements associated with the production of acoustic signals), or independent signals in different modalities that are sometimes produced simultaneously (Figure 12.2). The functions of the different components of multimodal signals vary; for example, they may be redundant (evoking similar responses from the receiver), additive (the response to the combination equals the sum of responses to each separate component), or interact in nonlinear ways (Hebets and Papaj 2005; see also Box 12.1).

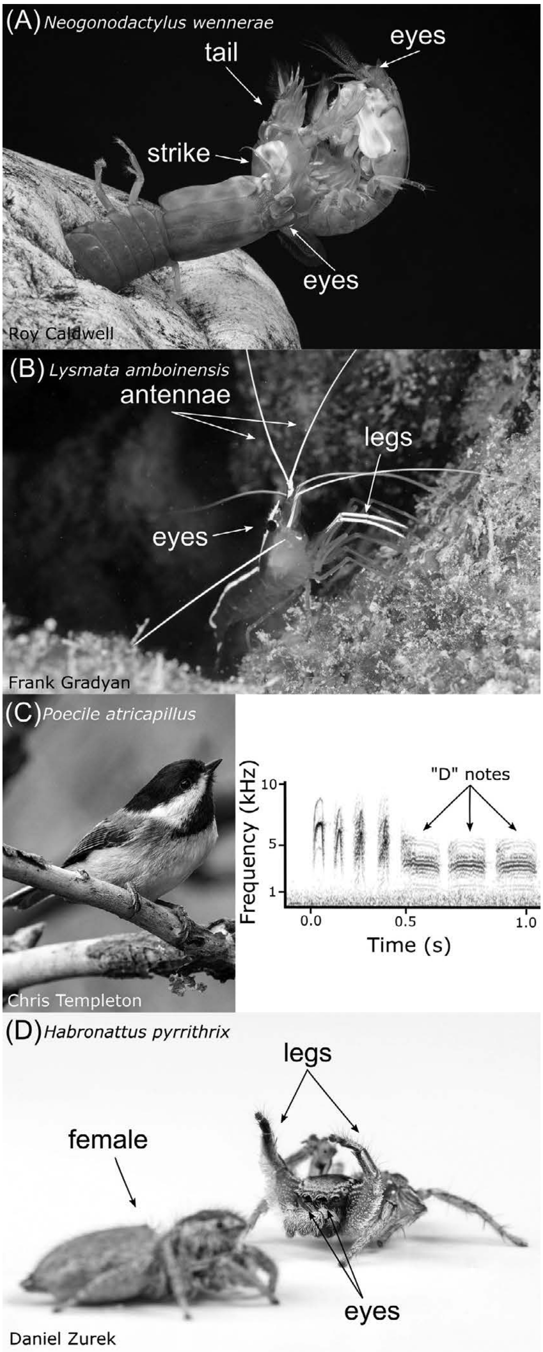

Figure 12.2 Signal diversity varies across taxa and sensory modality, as well as other factors. (A) Competing mantis shrimp use tactile signals during contests over territory. Here, the signaler (left) strikes the coiled tailplate of the receiver (right). (B) Cleaner shrimp use dynamic visual signals (waving white legs) to signal their intent to remove parasites from client fish. (C) Black-capped chickadee vocal signals consist of introductory notes followed by repeated "D" notes. The order and repetition of notes are characteristics of this signal assessed by receivers. (D) Many spiders, such as male jumping spiders, use a combination of static (color patches) and dynamic (e.g., waving legs) visual signals, as well as mechanoacoustic signals, when courting females (reviewed in Herberstein et al. 2014).

Box 12.1 Case study of signals and signaling: snapping shrimp open claw displays

Snapping shrimp (*Alpheus* spp.) are small crustaceans with highly asymmetric claws. The larger claw produces a loud snap when rapidly closed, and can be a deadly weapon. Nonetheless, body size (rather than claw size) predicts the outcome of conspecific contests (Hughes 1996a).

Signals & signalers

Both male and female shrimp perform "open claw" visual signals. Claw size is positively correlated with body size; the "open claw" signal, then, is an honest signal of body size, and shrimp respond to it as such (Hughes 1996a).

Variation in claw size independent of body size occurs for multiple reasons. Shrimp differentially invest in claw growth seasonally: males increase claw size relative to body size during the reproductive season, but females do so in the nonreproductive season (Heuring & Hughes 2019). Claws lost due to fights or attempted predation require at least 3 months to regain full size (Pereira et al. 2014), so claw size also depends on recent experience.

Variation in claw size independent of body size provides opportunities for some signalers: males with larger claws than predicted for their body size perform more open claw signals, deceptively signaling larger body size (Hughes 2000). Signal use, in other words, depends on the degree to which the signal exaggerates apparent size.

Multimodal signaling

The open claw visual signal can be combined with chemical signals, producing interactive effects. When received with male chemical signals, males respond with increased, size-independent aggression. Conversely, when combined with female chemical signals, males respond with lower, size-dependent aggression (Hughes 1996b).

The snap may also be a multimodal signal: the rapid closure of the claw produces both a fast water jet and subsequent cavitation bubble collapse and snap. The water jet is highly directional; shrimp aim the jet at opponents in competitive interactions (Herberholz and Schmitz 1998). However, when pairing with males, female shrimp often snap directly away from the male, suggesting assessment of the signal may depend on which components (water jet with or without sound) are received (Hughes et al. 2014).

Bias in studying animal signals

Males have larger claws than females, a sexual dimorphism typically attributed to sexual selection. However, larger claws do not appear to benefit males in reproduction (Hughes et al. 2014). Moreover, females are more aggressive than males: females snap more than males in aggressive interactions (Hughes et al. 2014), and are more likely than males to kill their opponents (Knowlton and Keller 1982). Differential investment in claw growth in the nonreproductive season suggests larger claws are advantageous to females but costly during the reproductive season, when they are often carrying thousands of eggs (Heuring and Hughes 2019). Thus, sexual dimorphism in claw size may be driven as much by greater costs of larger claws to females as by greater benefits to males. Gendered expectations (as well as other unconscious biases) of behaviour may affect both what signals are studied, and what hypotheses are tested (see, e.g., Haines et al. 2020).

Signals are often produced in sequences. As with multimodal signals, each signal in a sequence may contribute differently to the receiver's response. For example, to alert receivers to the presence of predators, birds in the family Paridae produce a "chickadee" call composed of introductory notes followed by a series of "D" notes. Information is encoded in this call in a variety of ways, including which notes are included and in what order (Suzuki et al. 2016), and the number of note repetitions within the call (Templeton et al. 2005; Figure 12.2C).

Identifying and analyzing signals, then, is an inherently hierarchical process. As illustrated with the fictional color patch example above (see also Box 12.1), even relatively simple signals are composed of numerous (potentially independent) characteristics that could elicit a receiver response. The response may also depend on other signals presented simultaneously or in sequence. Determining which signal characteristics are salient to receivers and how receivers respond to the presence or sequence of other signals is a key question in any communication system.

How is signal form related to function?

Consider the color patch example above. If color patch size signals competitive ability, receivers might respond by retreating from signalers with larger patches, but by attacking signalers with smaller patches. In this scenario, poor competitors would benefit by signaling dishonestly: displaying large color patches in spite of low competitive ability. Clearly, if such dishonesty occurs too often, receivers will no longer be able to use the signal to gain reliable information about the signaler and the communication system should break down. What keeps signalers honest, even when dishonesty could benefit signalers?

When dishonesty could benefit signalers, fitness costs of signaling are fundamental to maintaining signal honesty. Precisely how costs maintain honesty, however, remains disputed (Penn and Számadó 2020). The long-held consensus (see Searcy and Nowicki 2005) is that honesty is maintained by fitness costs that increase with some aspect of signal production (e.g., color patch size). However, such costs paid by honest signalers may be unnecessary as long as dishonesty is costly (Hurd 1995; Higham 2014) – that is, honestly producing large or small color patches need not require different fitness costs, as long as dishonestly producing large color patches is costly. Understanding the relationship between signal costs and honesty, then, may require examining costs specifically in dishonest signalers.

In theoretical models, the costs involved in maintaining signal honesty are related to fitness; for example, the number of surviving offspring the signaler produces. However, in practice these costs are often inferred from physical or physiological links between the information assessed by receivers and underlying variation in the signaler's internal state and/or external morphology that limits signal production (Figure 12.1B). Many signals are condition-dependent in their expression, with signal structure correlating with aspects of signaler health, such as parasite load (e.g., in turkeys *Meleagris gallopavo*, the size of their long, fleshy forehead structure, Buchholz 1995). Aspects of both visual signals (Box 12.1) and acoustic signals (Davies and Halliday 1978) are often constrained by – and so can be honest signals of – body size. Stressors encountered during development affect both the brains and songs of adult songbirds; song, then, is an honest signal of developmental condition (Nowicki and Searcy 2004).

Dishonest signalers also may incur costs resulting from receiver responses. Dominant Harris Sparrows (*Zonotrichia querula*) have larger areas of black breast plumage than subordinates; experimentally created "cheaters" received more attacks after their black spots were enlarged (Rohwer 1977). In many songbirds, singing low amplitude songs is a reliable signal of attack, and similarly carries a high risk of retaliation from receivers (Akçay et al. 2015). These signals are not physically or physiologically constrained to be honest, but dishonest signalers risk provoking a costly receiver response.

While dishonest signaling is generally limited by its costs, it is not fully prevented. For example, newly molted (and thus unable to fight) mantis shrimp (*Neogonodactylus bredini*) will signal aggressively when their opponent is smaller – that is, when the opponent is unlikely to call their bluff (Adams and Caldwell 1990). The imperfect relationship between signal characteristics and information assessed by the receiver can also provide opportunities for signalers to exaggerate that information (Box 12.1). For signalers, tradeoffs between eliciting beneficial responses from receivers and the potential costs of dishonest signaling can result in low levels of deception persisting in otherwise honest signaling systems.

Finally, for many signals, costs are unnecessary to prevent dishonesty because signalers and receivers have the same interests with regard to the outcome of the interaction; in other words, these signals are used in contexts where deception would not benefit signalers. For example, honey bees (*Apis mellifera*) perform a dance to signal the location and quality of food sources to hive-mates (von Frisch 1967), and vervet monkeys (*Chlorocebus pygerythrus*) produce acoustically distinct alarm calls to signal different predator types to group-mates (Seyfarth et al. 1980). In these cases, the optimal response (find food or escape predation) is the same for both signaler and receiver.

How, then, is signal form related to function? Aside from signals for which physical or physiological links between the signaler and signal information are necessary to maintain honesty, the relationship between signal form and function may be largely arbitrary (Nowicki et al. 1992), as typically assumed for human language (but see Blasi et al. 2016). Alternatively, there may be general principles with regard to signal form/function relationships that have yet to be explored. Absent these general principles, both correlative and experimental work on this relationship risks being a fishing expedition, and can be dangerously susceptible to bias (Box 12.1).

II. Signal transmission

All signals, except tactile signals, pass through the environment before reaching the receiver, and thus are subject to environmental effects during transmission. These effects depend on physical characteristics of both the signal and the environment: in densely vegetated habitats, acoustic signals reverberate more (masking rapid temporal patterns), and lower frequency signals propagate further than higher frequency signals; differences in ambient light across habitats – including increasing depth in aquatic habitats – lead to differences in apparent color; and the distribution of chemical signals depends on speed and turbulence of the media (Bradbury and Vehrencamp 1998).

Signals can also be masked by ambient noise, including abiotic sounds (wind, rain) and sounds produced by other organisms (Naguib 2013). In some cases, selection to minimize overlap between signals may result in the partitioning of signal transmission space, similar to ecological resource partitioning (for example, species-specific acoustic niches, Chitnis et al. 2020).

Many signalers modify signal production according to environmental effects on transmission. For example, some birds choose display locations that maximize the visual contrast of their color signals (Endler and Théry 1996). Signalers may also modify the transmission characteristics of their environment. For example, many aquatic animals produce flows to enhance or direct the transmission of chemical signals (Atema 1995); tree crickets (*Oecanthus henryi*) chew holes in leaves, creating structures that increase call amplitude (Deb et al. 2020).

Another environmental feature that impacts communication systems is unintended receivers that intercept signals during transmission (eavesdroppers): potential rivals, predators, parasites, etc. For example, male túngara frogs (*Engystomops pustulosus*) produce "whine-chuck" calls to attract females; females prefer calls with more "chucks", but this call component also makes the calls more conspicuous to predatory bats and blood-sucking flies (reviewed in Ryan 2011). Negative effects of eavesdropping on signalers and intended receivers may lead to the evolution of "private communication" channels that are potentially less vulnerable to eavesdroppers (see Section III).

III. Receivers & responses

To elicit responses, signals must be detected by the receiver's sensory organs, discriminated from other stimuli, and recognized as signals. Thus, receiver sensory capabilities and perceptual processes are important selective forces in signal evolution.

Sensory capability

Animal sensory capabilities are extremely diverse (Stevens 2013): many animals perceive stimuli in sensory modalities that humans cannot (e.g., magnetic and electric fields), and for modalities we share, animals may perceive a wider range of stimuli (e.g., ultraviolet and ultrasonic stimuli). Conversely, some species may not perceive sensory information that humans can (Figure 12.3). Signals must be detectable by the sensory system of the intended receiver(s), but beyond detectability, how and in what ways do sensory systems place selection pressure on signal form?

The sensory drive hypothesis (Endler 1992) predicts that signals should evolve to be detectable by receiver sensory systems specifically in the environment in which communication occurs. For example, the scarab horned beetle (*Coprophanaeus lancifer*) is a violet-blue species that searches for mates at dusk. The beetle's body coloration appears tuned for visual detection by conspecifics at short distances in the beetle's forest understory habitat, specifically at dusk (Théry et al. 2008).

The sensory exploitation hypothesis (reviewed in Taylor and Hunter 2016) states that pre-existing receiver biases toward non-signal stimuli can, over evolutionary time, be exploited by signalers. For example, in water mites (*Neumania papillator*), males seeking a mate mimic the vibrations made by copepod prey. Hungry females are more likely to respond to male signals, and male signals evolved after water mites started using vibrational cues to locate prey (Proctor 1992). Thus, male water mites exploit a female sensory bias that evolved in the context of foraging. Signalers can also exploit pre-existing receiver responses to predators, protective structures, or potential mates (Taylor and Hunter 2016).

Signal form can also evolve to exploit differences in sensory capability between potential receivers, such that signals are more apparent to intended than unintended (usually heterospecific) receivers

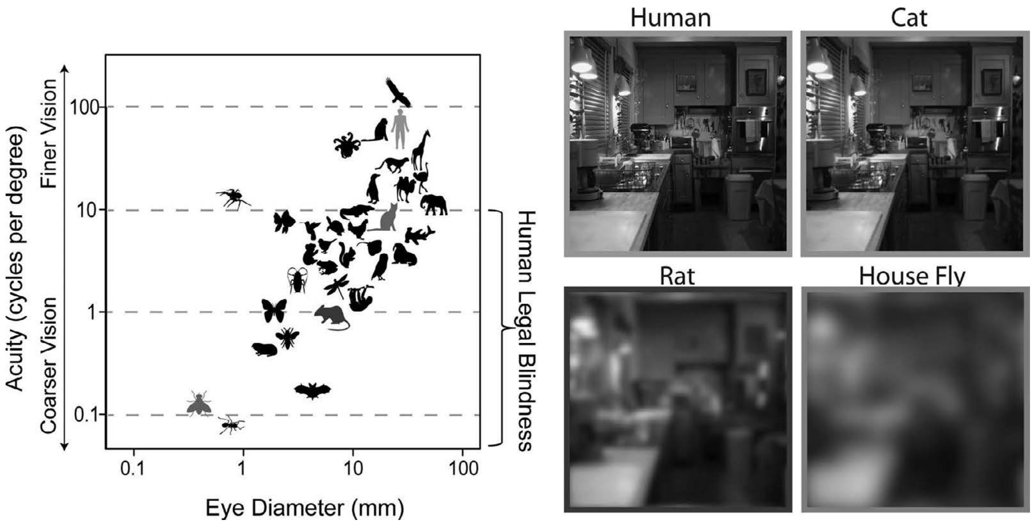

Figure 12.3: Visual acuity, the ability to perceive static spatial detail, ranges over four orders of magnitude. (Left) Acuity, measured in cycles/degree (the number of black and white stripe pairs an animal can resolve in one degree of visual angle) is highly correlated with eye size (Caves et al 2018a). Humans (light grey) have some of the highest acuity in the animal kingdom. (Right) Variation in visual acuity likely translates to differences in how species perceive the spatial aspects of scenes and signals, as illustrated by this kitchen scene filtered through the visual systems of four potential kitchen inhabitants. Left: modified from Caves et al 2018a. Right: original image by F Deventhal - flickr, CC BY 2.0 (https://commons.wikimedia.org/w/index.php?curid=7514374), modified using AcuityView (Caves and Johnsen 2017).

(e.g., eavesdroppers). These "private signals" have been proposed in nearly every sensory modality and across many taxa. Examples include UV signals in courting swordtail fish (*Xiphophorus nigrensis*), biphasic electric signals in weakly electric fish (family Gymnotidae), and ultrasonic soft songs in moths (*Ostrinia furnacalis*) that may be less detectable to predators than to intended conspecific receivers (reviewed in Brandley et al. 2013).

Perceptual processing

Following signal transduction by sensory organs, sensory information may be modified by perceptual processes, with effects including changes to signal detectability, discriminability, or memorability; discontinuous perception of continuous variation (see below); grouping or segregating stimuli to form perceptual objects; and integration of multi-modal signals (reviewed in Miller and Bee 2012).

One group of signals for which perceptual processes, such as detection and memory, have been well-studied are aposematic, or warning, signals. Many toxic or distasteful animals display bright, conspicuous color patterns that signal their noxious odors or tastes. These signals are highly detectable and memorable by predators, allowing them to quickly learn to avoid aposematic prey (reviewed in Speed 2000).

Signalers may also manipulate receiver perceptual processing. Male great bowerbirds (*Chlamydera nuchalis*) display to females on elaborate courts, which they cover with objects like stones and bones. Males arrange these objects such that, as distance from the female's viewing position increases, so does the object's perceived size. This arrangement creates a visual illusion known as forced perspective, which can affect the viewer's perception of size. Males that more successfully construct this illusion have higher mating success (Kelley and Endler 2012).

Categorical perception

Among-individual variation in signal characteristics – size, hue, frequency, etc. – is often continuous. However, receivers may sort continuous variation in a stimulus into categories in a phenomenon called categorical perception (reviewed in Green et al. 2020). Here, receivers (1) label a continuous range of stimuli as belonging to different categories, and (2) exhibit an increased ability to discriminate between stimuli from different categories, relative to equally-different stimuli from the same category. Thus, certain stimulus variants are perceived as more or less distinct from one another than we might otherwise predict.

Although categorical perception was first described in the context of human discrimination of speech phonemes, humans also categorically perceive color, and it was long thought that language was crucial for structuring color categories, making categorical perception of color a uniquely human phenomenon (see Green et al. 2020). This view has recently been challenged, in part through work on the zebra finch (*Taeniopygia guttata*).

In human studies, demonstrating categorical color perception involves asking subjects to describe what group a stimulus belongs to (for example "blue" or "green"). In non-human animal studies, other methods must be devised to determine if an animal perceives stimuli as "same" or "different." Caves et al. (2018b) tested female perception of male beak colors – a mate choice signal that varies continuously in males from light orange to dark red (Collins and ten Cate 1996) – by training females to remove colored discs to access food rewards. Discs were made using eight colors that parallel the range of variation in male beaks and that are equally distinct from one another to a zebra finch visual system. Discs were either solid or bicolor (see Figure 12.4A), but only bicolor discs were rewarded. Over time, finches learned to search for food beneath discs that they perceived as comprising two different colors. By varying the colors on the bicolor disc, the researchers showed both features of categorical perception: females labelled the orange-red continuum as lying in two discrete categories, and female ability to discriminate between colors was higher when colors came from different categories

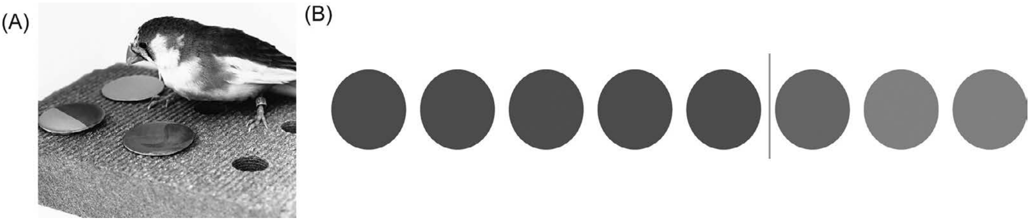

Figure 12.4 (A) A female zebra finch performs a perceptual task by flipping discs made of colors along a (B) orange-red continuum. Vertical line shows category boundary in Caves et al. (2018b).

Photo by Ryan Huang, Terra Communications LLC.

compared to when they came from the same category (Caves et al. 2018b). Thus, the perceptual system of female zebra finches may sort males into categories: low quality 'orange' males and high quality 'red' males (Figure 12.4B). In contrast, Bengalese finches – a related species that does not use orange-red signals in mate choice – do not exhibit categorical perception of these colors. This latter result supports the hypothesis that selection on communicative function shaped categorical perception in zebra finches (Caves et al. 2021).

Influence of environment and internal state on receiver assessment

While controlled behavioural assays or studies of sensory receptor physiology are powerful tools by which to probe perceptual processes in non-human animals, results from such experiments do not fully predict signal assessment in nature due to extrinsic factors (such as social environment) or variation in intrinsic state.

The presence of other conspecifics is one such extrinsic factor. Female fiddler crabs (*Uca mjoebergi*) prefer males with larger claws relative to surrounding males. As a result, the same male may be preferred when adjacent to smaller-clawed males, but not when his neighbors have larger claws (Callander et al. 2013). Receivers may also alter their responses after observing other receivers. Female guppies (*Poecilia reticulata*) that previously rejected a male, for example, treat that male as more attractive after watching him being chosen by a different female (Dugatkin 1992).

Internal states, such as motivation or signal response thresholds, can change over time, potentially leading to changes in receiver responses. For example, female field crickets (*Gryllus lineaticeps*) prefer males that produce calls with chirp rates above 3/second; however, as more time elapses since exposure to any preferred male, females become more accepting of males with chirp rates below this threshold (Beckers and Wagner 2011). Thus, females alter their acceptance thresholds for otherwise undesirable males to secure reproductive opportunities.

IV. Signaling interactions

How the signaler and receiver interact after the signal is received is a crucial link in communication. If receiver responses did not, on average, benefit the signaler, the communication system would break down (Searcy and Nowicki 2005). Receiver responses can include a wide range of behaviours, including mating with or not eating the signaler, and/or producing signals themselves, leading to an exchange of signals.

Animal contests over resources like territory or mates provide well-studied examples of signaling interactions. Models of these signaling interactions suggest that signals allow competitors to gather information on competitive ability and decide whether to stay in the fight or give up (reviewed in Arnott and Elwood, 2009). In the Sequential Assessment Model (SAM), the information a receiver first gathers about its opponent's ability from a signal is imperfect or incomplete. By signaling in response, the receiver elicits another signal from the signaler and improves the information it has on signaler ability (a process akin to statistical sampling). Competitors may repeat this cycle several times with the same signal, or may escalate to producing a different signal that gives more accurate information than the first but that may come with a higher cost (e.g., in terms of energy or risk of injury). When one individual gathers sufficiently accurate information to determine it is the weaker competitor, it leaves the contest. In contests between male red deer (*Cervus elaphus*), for example, signalers progress from exchanging 'roar' vocalizations, to 'parallel walking' visual displays, to physical fighting by 'antler sparring' (Clutton-Brock and Albon, 1979).

Alternative theoretical models propose that competitors don't gather any information on relative ability from repeated signals. Instead, signals may function in a 'war of attrition' such that whoever can produce these repeated signals (and withstand their energetic or other costs) for longer wins. Some repeated behaviours during contests may be used simply to inflict injury to opponents, without having any signaling function (Arnott and Elwood, 2009).

New analytical approaches have advanced our understanding of signaling interactions during contests. For example, Green and Patek (2018) adapted network analysis techniques from the social sciences to statistically analyze the progression of contest behaviours in mantis shrimp (*Neogonodactylus bredini*), which use visual displays and high-force strikes during contests over burrows. These strikes are extremely powerful; they are also used to crack open hard-shelled prey like snails. However, in contests, strikes are exchanged on competitors' armored tailplates (Figure 12.2A), suggesting a communicative function (Green and Patek, 2015). Competing individuals progress from visual displays to the exchange of strikes, which leads to contest resolution. These progressions match the predictions of the SAM, suggesting that strikes aren't used simply to inflict injury, but instead to gather information on relative ability (Green and Patek 2018). Biomechanical modeling and high-speed video analyses found that the energy mantis shrimp use to power their strikes, and therefore the energy a competitor receives from a strike, can communicate a striking individual's body size (Green et al. 2019). Body size is an important metric in these contests, but is hard to assay visually as one competitor is often in a burrow. Thus, the ritualized exchange of strikes in mantis shrimp may allow for tactile assessment of ability (Green and Patek, 2018).

Impacts of receiver responses on subsequent signaler behaviour, including signal exchanges, are not limited to contests. Male satin bowerbirds (*Ptilonorhynchus violaceus*) signal to females using repeated, dramatic displays – including puffing out their feathers, vocalizing, and flaring their wings – that are similar to aggressive signals and so potentially startling to females. Males may reduce their display intensity in response to female startle behaviour, and males who produce more intense displays while minimizing female startle responses have highest courtship success (Patricelli et al. 2002). Signal exchanges can also occur between different species, as in cleaner shrimp and client fish – many of which are potential predators (Figure 12.2B). Cleaner shrimp (*Ancylomenes pedersoni*) signal motivation to clean (i.e., remove parasites from) the client by flicking their antennae. When cleaners don't signal first, clients can sometimes induce cleaning by rapidly changing to a dark color morph, a signal of their own (Caves et al. 2018c). These examples highlight that communication is unlikely to be fully characterized by the one-way signaler-receiver process diagrammed in Figure 12.1; understanding the dynamics of signaling interactions remains a fundamental question in animal communication.

V. Future directions

Critical questions

Throughout this chapter, we've highlighted many areas where critical questions remain to be addressed. While much work on signal production has focused on the costs necessary to maintain honesty, an open area of debate is when we expect such costs to be evident. Furthermore, for signals not physically or physiologically costly to the signaler, we lack a theoretical framework by which we can predict the form of a signal from the information it contains (or vice versa). The investigation of signal function, then, can be dangerously open to correlative fishing expeditions and experimenter bias (Section I). While animal communication researchers have long recognized that non-human perceptual systems differ from our own, current work expanding beyond signal reception to perceptual and cognitive processing of signals will provide better insight into the role of the receiver as a selective force on signal design (Figure 12.1B, Section III). Lastly, our expanded methodological toolbox will allow an understanding of signal function in more realistic, dynamic exchanges. For example, new analytical approaches (Section IV) provide new insights into both new and longstanding questions. As another example, remote recording technologies – both stationary and those attached to the animals themselves – will increasingly allow us to observe in situ behavioural interactions over longer time scales and without the confounding presence of a human observer, producing large amounts of real-time, fine-scale data on animal movements, social interactions, and signal production and responses.

Applications: non-human communication in a human-modified world

Another area of research that is increasingly important is the impact of anthropogenic effects on animal communication. Similar to other environmental effects on transmission, human activities can generate noise that masks and/or modifies animal signals. For example, weakly acidic conditions cause covalent changes to some fish chemical signals, rendering them less effective (Brown et al. 2002). Anthropogenic noise masks a wide range of signals: traffic noise overlaps bird song, artificial lighting obscures the signal flashes of glow worms, and increased turbidity in aquatic environments makes color signals less visible (Candolin 2019). Anthropogenic environmental changes may also induce shifts to novel habitats, resulting in changes in signal transmission (Caves and Johnsen 2021).

Anthropogenic effects on signal transmission may result in changes to signal structure or signaling behaviour. In the presence of traffic noise, for example, many songbirds shift song frequency or timing (Candolin 2019). During the 2020 coronavirus pandemic, white-crowned sparrows quickly filled the quiet left by lack of human activity and resumed singing at frequencies usually masked by traffic noise (Derryberry et al. 2020).

Anthropogenic effects on communication are not limited to those affecting signal transmission. Many pollutants alter signal production and/or receiver responses to signals (reviewed in Candolin 2019). Some of these effects may reflect underlying changes in physiology and/or cognitive processes. For example, juvenile damselfish learn an anti-predator signal by observing conspecifics, but after four days of exposure to ocean acidification conditions, damselfish were unable to learn anti-predator behaviours, perhaps because neural changes disrupted learning (Ferrari et al. 2012). Sometimes, receivers even mistake anthropogenic pollutants for signalers. Male jewel beetles, for example, confuse discarded beer bottles with females and attempt to mate with them (Gwynne and Rentz 1983).

Given these wide-ranging anthropogenic effects on signal transmission and receiver responses, downstream effects on signaling interactions – and as a result, on reproductive and social behaviour more broadly – seem likely. Thus an understanding of how human-dominated environments alter signaling dynamics is critical for managing our impacts on other species in an increasingly human-modified world.

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13

INTRASPECIFIC AGGRESSION AND SOCIAL DOMINANCE

Christine M. Drea and Nicholas M. Grebe

Historical Perspectives and Definitions

Aggression is a broad category of animal behaviour, with a long history of study (Box 13.1). It takes many forms, can be overt or covert, integrates numerous biological mechanisms, and serves various functions, immediately raising definitional issues (Baron and Richardson 2004): Broadly, aggression is evidenced as any behaviour (often forceful, physical action) by which an individual self-asserts, dominates or inflicts harm upon another individual "motivated to avoid such treatment." In nature, clear elicitors of aggression, such as attacks or territorial incursions, provide insight into functional categorizations: e.g., predatory or anti-predatory, defensive or fear-induced, resident-intruder, protective or maternal, and siblicidal or infanticidal. Under more controlled conditions, experimental manipulation provides further insight about context specificity, such as density-dependent aggression from crowding or social isolation, and about pharmacologically induced or brain-stimulated aggression. Aggression involves few 'reflexive' responses; context dependence and facultative responsivity is the general rule.

Here, we focus on intraspecific, vertebrate aggression, particularly intra- and intersexual aggression in the Darwinian context of resource competition, including over mates (Box 13.1). Intricately linked to such incentivized competition are dominance relations between members of socially integrated groups that substitute overt aggression with ritualized displays or subordination. Accepted rank relations can minimize damaging, stressful, and divisive effects of aggression, while likewise relating to reproductive success in certain species (Dewsbury 1982). Given the many approaches to studying these topics, we converge on a perspective rooted in behavioural ecology, adopting Tinbergen's (1963) four questions on causation, development, function, and evolution.

Intraspecific Competition and Reproductive Success

Darwin's (1871) theory of sexual selection provides the main adaptationist framework for considering the function of intrasexual aggression: differential reproductive success via competition over access to mates (Box 13.1). Because males are typically under the greatest selection pressure and show the most intense competition over mates (Andersson 1994), researchers emphasize the evolution of intrasexual male aggression and its covariates (Berglund et al. 1996). Secondary sexual characteristics or dimorphisms include sex differences in size, armaments, ornaments or signals that improve male competitive success, appeal to conspecific females, or reflect an arms race in male-female coevolution (Chapman et al. 2003). Particularly among mammals, sexual size dimorphism favors males

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Box 13.1 Historical and disciplinary highlights in the study of aggression

Late 19th Century: Early Darwinism and Intraspecific Competition

- Darwin (1871): Limited resources compel competition for survival and reproduction; individuals with more favorable adaptations to their physical and social environments supplant individuals lacking those features. Sexual selection can specifically entail aggressive or coercive intrasexual competition for mates.

Early 20th Century: 'Nature-Nurture' Debates

- Early perspectives in recurring debates over the extent to which aggression is learned vs. innate often implicitly dichotomize these possibilities, but later developments outline the importance of their interactions.

Perspectives on an aggressive instinct

- Freud (1930): Aggression results from an innate force—the 'destructive instinct' (*Thanatos*)—in perpetual conflict with an opposing 'life instinct' (*Eros*). Human culture creates rules that manage animalistic aggressive instincts.
- Lorenz (1963): Aggression is an instinctual 'survival trait,' particularly in males, allowing only the fittest individuals to reproduce.

Behaviourism and social learning theories

- *'Behaviorist manifesto'* (Watson 1913): 'Laws of behavior' dictate that prediction and control of all animal behaviour (including human aggression) occur via conditioning.
- Frustration-Aggression Hypothesis (Dollard et al. 1939): Organisms are motivated to achieve their goals (e.g., escape a threat); when pursuit of those goals is blocked, aggression ensues.
- Operant Conditioning (Skinner 1953): Organisms modify the frequency of their responses (including aggression) in relation to reward or punishment.
- Social Cognitive Approach (Bandura 1965): Aggression is shaped by cognitive 'scripts' acquired from early acculturation or socialization processes, whereby individuals experience positive reinforcement for aggression or learn to imitate aggressive models.

Late 20th Century: Comparative and Evolutionary Perspectives by Discipline

- Behavioural Ecology: Trivers' Parental Investment Theory (1972) predicts the sex that invests least in offspring engages in relatively more intrasexual competition; his Parent-Offspring Conflict Theory (1974) proposes an inherent source of conflict within family units over optimal parental investment.
- Sociobiology: Humans (as animals) have an innate capacity for various kinds of aggression that serve various biological functions; yet, responses are labile and there is no general 'aggressive instinct' (Wilson 1978).
- Primatology/Anthropology: Post aggression, competitors *reconcile* to mend broken bonds, and *console* or reassure onlookers, suggesting a delicate balance between conflict and prosociality (de Waal and van Roosmalen 1979). Comparative studies within great apes show that violence in men is an evolutionary, but not insurmountable, legacy (Wrangham and Peterson 1996).

- Evolutionary Psychology: Beyond differences in mean frequency or intensity of aggression, distinct (but overlapping) styles are identified between the sexes, with males favoring violent, direct aggression (Daly and Wilson 1994) and females favoring indirect or social aggression (Vaillancourt 2005).
- Social Psychology: Scholars increasingly favor a functional approach, showing that aggression is one of several possible 'influence strategies' to pursue goals (Krahé 2013).

Cusp of the 21st Century: Integrative Perspectives on Aggression

- Across disciplines (Behavioural Ecology: Clutton-Brock and Parker 1995; Economics: Fehr and Schmidt 1999; Social Psychology: Deutsch 2006), scholars increasingly recognize the inextricable links between competition and cooperation, and fairness and punishment. Rather than being oppositional, aggression is *necessary* for cooperation to evolve (Boyd and Richerson 1992).
- Contemporary research programs combine techniques (e.g., theoretical modeling, physiological manipulations, comparative or cross-cultural analyses), examine trade-offs, and integrate Tinbergian levels of analysis.

(Andersson 1994), but at the cost of delayed maturation and reproductive onset. Intrasexual male competition involving weaponry or size advantage can involve outright combat or more ritualized displays, particularly evident in individualized societies characterized by dominance hierarchies. In such cases, male reproductive success can be linked to dominance status more than to aggressive outcomes (Dixson 2013). Whether owing to wins or reputation, reproductive success and reproductive skew are often far greater in males than in females (Le Boeuf 1974).

Growing evidence supports more subtle, albeit equally powerful, modes of aggression, intrasexual competition, and differential reproductive success in females (Clutton-Brock 2009). Indeed, one of the most effective modes of reproductive competition, particularly in cooperatively breeding species, involves the matriarch's reproductive suppression of subordinate competitors, resulting in appreciable female reproductive skew (Solomon and French 1997). More generally, dominance relations translate to reproductive benefits evidenced as earlier age at menarche, shorter follicular cycles, shorter interbirth intervals, and greater offspring survival in dominant, relative to subordinate, females (Pusey et al. 1997). Females can also bear ornaments and weaponry, but these may mediate competition for ecological resources more than for mates and, thus, be socially rather than sexually selected (Tobias et al. 2012). In sum, there is significant evolutionary pressure in both sexes to improve survival and reproductive success via intra- and/or intersexual aggression. We now turn to the proximate mechanisms mediating such aggression.

The Vertebrate Neuroendocrine System

The origins of comparative neuroendocrinology

Prominent among the proximate mechanisms of aggression is the long-recognized role of male gonadal secretions: Aristotle (384–322 B.C.E.) had described the effects of castration across species, noting that gonadectomy rendered males more docile. In 1849, Berthold (as cited by Soma 2006) first tested the effects of removal, with or without replacement, of testicular tissue in cockerels (*Gallus gallus*), reporting that experimental males became capons, respectively possessing or lacking secondary sexual characteristics and associated behaviour. In complementary experiments, various steroids administered to chicks produced precocial display of these same traits (Breneman 1938). Such early studies helped formulate the original principle of endocrine action—that special organs (glands) pour their chemical secretions (hormones) directly into the bloodstream to exert distal morphological, physiological or behavioural effects.

Hormones can be excitatory or inhibitory and broadly include neurotransmitters and neurosecretions, together coordinating proximal neural and distal bodily functions across the animal kingdom (Hartenstein 2006; Figure 13.1). Initially, researchers anticipated consistent, unidirectional, dose-dependent effects of hormones, but even surgical castration can produce variable effects across individuals, owing to differences in age, status, sexual experience or motivation. Indeed, testosterone secretion in intact male primates can be modulated by social context, with a win or defeat respectively

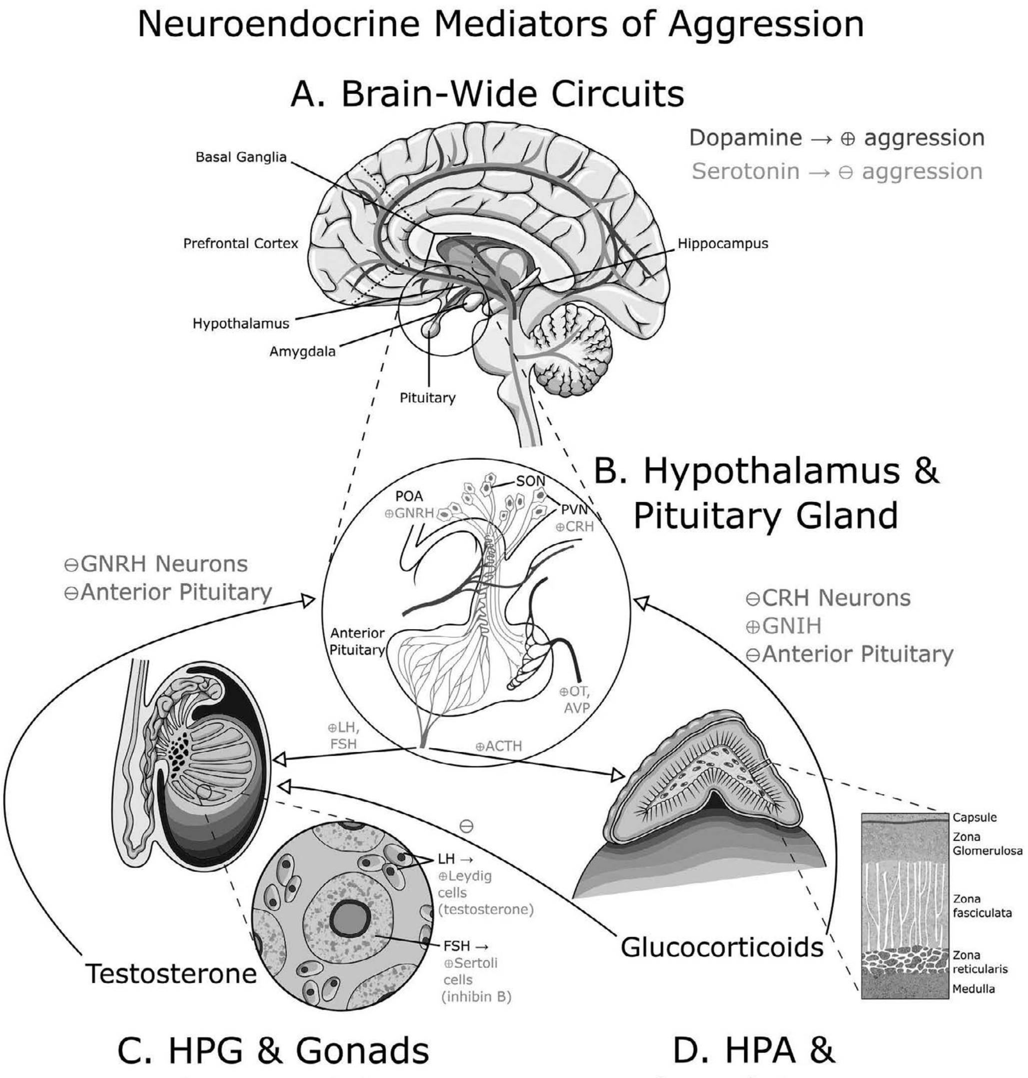

Figure 13.1 Representative neuroendocrine mediators of aggression in vertebrates. Shown for humans are (**A**) brain-wide dopaminergic and serotonergic circuits that typically have opposite influences on aggression; (**B**) intimate connections between the hypothalamus and pituitary, particularly in relation to the (**C**) hypothalamic-pituitary-gonadal (HPG) axis, illustrated for males, and (**D**) hypothalamic-pituitary-adrenal (HPA) axis. ⊕ for activation; ⊖ for suppression; see text for abbreviations..

Drawings adapted by S. Bornbusch.

preceding a rise or fall in concentrations (Rose et al. 1972). By extension, although social status can be determined by physical competition, there is also evidence for reversed patterns: changes in physiological condition can precede status changes. Beyond the importance of experiential factors and the permissive role of hormones in bi-directional relations with behaviour (Sapolsky 1997), endocrine action in vertebrates is homologous in males and females (Albert et al. 1992). All classes of sex steroids (progestins, androgens, and estrogens) are involved in mediating aggression, but sensitivities and responsiveness are intricately connected to genetically defined processes that vary by species, sex, season, and individual (McCarthy and Arnold 2011).

Brain regions and neurotransmitters associated with aggression

The amygdala and hypothalamus are two prominent brain areas involved in regulating vertebrate aggression (Figure 13.1A). The amygdala mediates the perception of and reaction to aggression (Haller 2018), such that stimulating or lesioning this area, respectively, increases or decreases aggression (Gouveia et al. 2019). Stimulating the hypothalamus also elicits aggression, but this region is best recognized for its density of receptors that respond to neurotransmitters, including dopamine, serotonin, norepinephrine, and γ-aminobutyric acid, involved in regulating mammalian aggressive responses (Narvaes and de Almeida 2014). Whereas dopaminergic action is typically associated with increasing aggression, and serotonergic action is typically associated with decreasing aggression (Popova 2006; Figure 13.1A), recent findings increasingly reveal the complexity of these neuromodulatory processes. For example, repeat activation of rodent oxytocin (OT) neurons, present in both the supraoptic nucleus (SON) and paraventricular nucleus (PVN) of the hypothalamus, can have different prosocial versus agonistic effects depending on social context (Anpilov et al. 2020). Likewise, three opioid families (endorphins, enkephalins, and dynorphins) often known to decrease aggression, also show genetic sources of variation in intermale aggression (Tordjman et al. 2003).

The hypothalamic-pituitary axes

The 'Hypothalamic-Pituitary-Gonadal' (HPG) axis. Regulated via feedback loops (Figure 13.1B, C), sex steroids are intricately linked to vertebrate reproductive and aggressive behaviour. Pulsatile release of gonadotropin-releasing hormone (GnRH), synthesized in neurons of the preoptic area (POA) of the hypothalamus, stimulates synthesis and release of the gonadotropins, follicle-stimulating hormone (FSH) and luteinizing hormone (LH), from the anterior pituitary. In both sexes, LH stimulates androgen production in the gonads, which, in conjunction with gonadotropic inhibiting hormone (GnIH), generally has a negative feedback effect on GnRH. Mounting evidence shows that the entire HPG axis is neuronally plastic in response to changes in the social environment. For example, soma size of GnRH-expressing neurons varies rapidly with acquisition of dominance status in teleost fish (Maruska 2014).

The 'Hypothalamic-Pituitary-Adrenal' (HPA) axis is the major stress response system of vertebrates (Figure 13.1B, D). The stress response begins in the PVN, where neuroendocrine neurons synthesize and release arginine vasopressin (AVP) and corticotropin-releasing hormone (CRH) that together stimulate the anterior pituitary gland to synthesize and release adrenocorticotropic hormone (ACTH). In response to ACTH, cells in the adrenal cortex secrete the glucocorticoid hormones cortisol and/or corticosterone. Once in circulation, glucocorticoids produce a negative feedback cycle acting on the hypothalamus and pituitary to suppress CRH and ACTH production (Selye 1950). While activation of the HPA axis is adaptive for 'flight or fight' responses and for maintaining homeostasis, chronic stressors can elicit a suite of negative consequences to an animal's health, behavioural repertoire, and reproductive potential, highlighting an important balance between activation of the HPG and HPA axes.

Integrative Behavioural-Endocrine Frameworks

The Challenge Hypothesis

To maximize reproductive success, individual organisms navigate a balance between investment in mating versus parenting. With mating effort, males of many species emphasize finding and attracting partners and competing with rivals for mating opportunities, via increased aggression, risk-taking, and investment in costly ornamentation. In contrast, with parenting effort, individuals invest time and resources into long-lasting, stable mating relationships and offspring care, either through provisioning or rearing. Although both strategies can increase reproductive fitness, there is an inherent tradeoff between the two, with allocation of energy toward one strategy reducing the pool of resources available for involvement in the other. Manifest in negative correlations between aggression and paternal care, this tradeoff arguably reveals 'constraints to the evolution of plasticity in aggression' (Duckworth 2006). In a wide variety of animal taxa, these shifts are mediated, at least in part, by the physiological and neuromodulatory effects of testosterone.

A theoretical model encompassing tradeoffs between reproductive strategies, and the role of testosterone during switch points, was first developed in avian seasonal breeders and dubbed the "Challenge Hypothesis." Wingfield et al. (1990) found that baseline testosterone concentrations increased at the start of the breeding season, which appeared to facilitate mate acquisition and territory formation. During confrontations with other males, testosterone concentrations surged from the new baseline to the physiological maximum; these surges predicted increased aggression, which aided in defending mates and territory. At the end of the breeding season, testosterone concentrations decreased as birds maintained their pair bonds and provisioned offspring. In short, these males were shifting between mating-dominant and parenting-dominant strategies, with testosterone fluctuations mediating the concomitant behavioural changes.

The Challenge Hypothesis has since spawned a large body of supporting evidence, from studies conducted at multiple levels of analysis, including inter-individual comparisons and examinations across multiple animal taxa. For instance, in teleost fishes and amphibian species, rises in testosterone and 11-ketotestosterone have been associated with dominance displays and increases in territoriality during the mating season, and in reptiles, testosterone is linked to male-male competition and social status (Moore et al. 2020). Both seasonally and aseasonally breeding primates show testosterone-mediated shifts between mating and parenting effort—a shifting pattern that is increasingly investigated in humans (Grebe et al. 2019c). Consistent with findings in other taxa, meta-analyses reveal generally modest, but statistically significant, associations between men's testosterone and aggression, risk-taking, and competition outcome (e.g., increases in testosterone after winning; Grebe et al. 2019a).

The Dual Hormone Hypothesis

Several non-significant associations between testosterone and male traits, such as dominance or aggression, nevertheless challenge the interpretation of testosterone as a straightforward predictor, leading researchers to seek alternate explanations. The "Dual Hormone" hypothesis has recently gained popularity in the human literature, positing that associations between testosterone and status-striving behaviour, such as aggression, are masked or at least rendered conditional by glucocorticoids (Mehta and Josephs 2010). This hypothesis accommodates evidence that the HPA and HPG axes can modulate one another (although the precise mechanisms and directionality of these interactions is a matter of ongoing debate; Grebe et al. 2019a), and that their interactions have consequences for downstream behaviour or psychological traits. The directional prediction for hormonal interaction involves high concentrations of glucocorticoids masking positive associations between testosterone and aggressive, status-seeking behaviour. This hypothesis has proven generative for human behavioural endocrinologists, but further comparative evidence, in addition to methodological and conceptual refinement (Grebe et al. 2019a), is needed.

‘Experiments of Nature:’ Mammalian Case Studies of Female Aggression

Although we generally lack understanding of the functional role of androgens in females (beyond aromatization to estrogens), vertebrate females vary substantially in their natural exposure to androgens (Staub and De Beer 1997), with potential benefits. In certain avian species, for example, maternal testosterone concentrations, deposited in yolk, correlate with the social rank and aggressive behaviour of juveniles (Schwabl 1993). Otherwise, aggressive females with raised androgens may experience reproductive costs, which can be induced experimentally via androgen administration (Rosvall et al. 2020). Nevertheless, sex role-reversed species, wherein female reproductive competition is more intense than in males, may show increased androgen concentrations and/or heightened sensitivity, and typically enjoy reproductive advantages. Because we lack understanding of the mechanisms to explain these profound species differences in female aggression and reproductive success, exceptional species provide unique opportunities to test sexual or social selection theories, particularly with regard to the neuroendocrine mechanisms that mediate behavioural sex differences (Eens and Pinxten 2000). Here, we examine exceptional mammalian species or ‘experiments of nature’ (Figure 13.2), in which female members are naturally physiologically, morphologically, and/or behaviourally ‘masculinized.’ Like males, they may also bear ornaments (Boulet et al. 2010) and experience costs of high androgens (Smyth et al. 2016). To provide a mechanistic framework for these studies, we begin with a brief review of mammalian sexual differentiation.

Sexual differentiation: organizational and activational effects of reproductive hormones

The mechanisms underlying sex differences in aggression are often overlooked in sexual selection studies, but are key to understanding the diversity and variability across species. Traditionally, differential expression of aggression has been linked to gonadal endocrine processes associated with sexual differentiation, originally conceived to explain differences in anatomical form and function. Notably, Jost (1947) identified a mechanism of mammalian somatic sex differentiation whereby male reproductive characteristics must be imposed on the fetus by two separate, active processes in the male involving testicular hormones, including ‘defeminization’ by anti-Müllerian hormone and ‘masculinization’ by testosterone. Without these hormones, fetal reproductive anatomy takes on a phenotypically female form. That female development need not be ‘induced’ in the same manner as male development led many to originally view female differentiation as an inherently passive process. Unconventional species have put our understanding of this process to the test and have shown that female development is neither passive nor a default condition (Drea et al. 1998). We now better recognize that primary sex-biasing influences are genetically encoded by the sex chromosomes, prior to hormone action (McCarthy and Arnold 2011).

In 1959, Phoenix, Goy, Gerall, and Young (as cited by Wallen 2009) expanded Jost’s formulation of sexual differentiation to the neural substrates underlying behaviour. By distinguishing organizational from activational effects of hormones, they transformed how we came to think about behavioural sex differences. It was already known that steroid hormones ‘activate’ typical patterns of male and female sexual behaviour, particularly at puberty, but Phoenix and colleagues showed that androgens, acting during critical and species-specific periods of development, also differentially ‘organize’ the structure and function of neural tissue, allowing later endocrine activation of adult behavioural sex differences – in e.g. mating, aggression, and rough play – under appropriate hormonal stimulation. These mechanisms provided new insight into developmental patterns, as certain behaviour

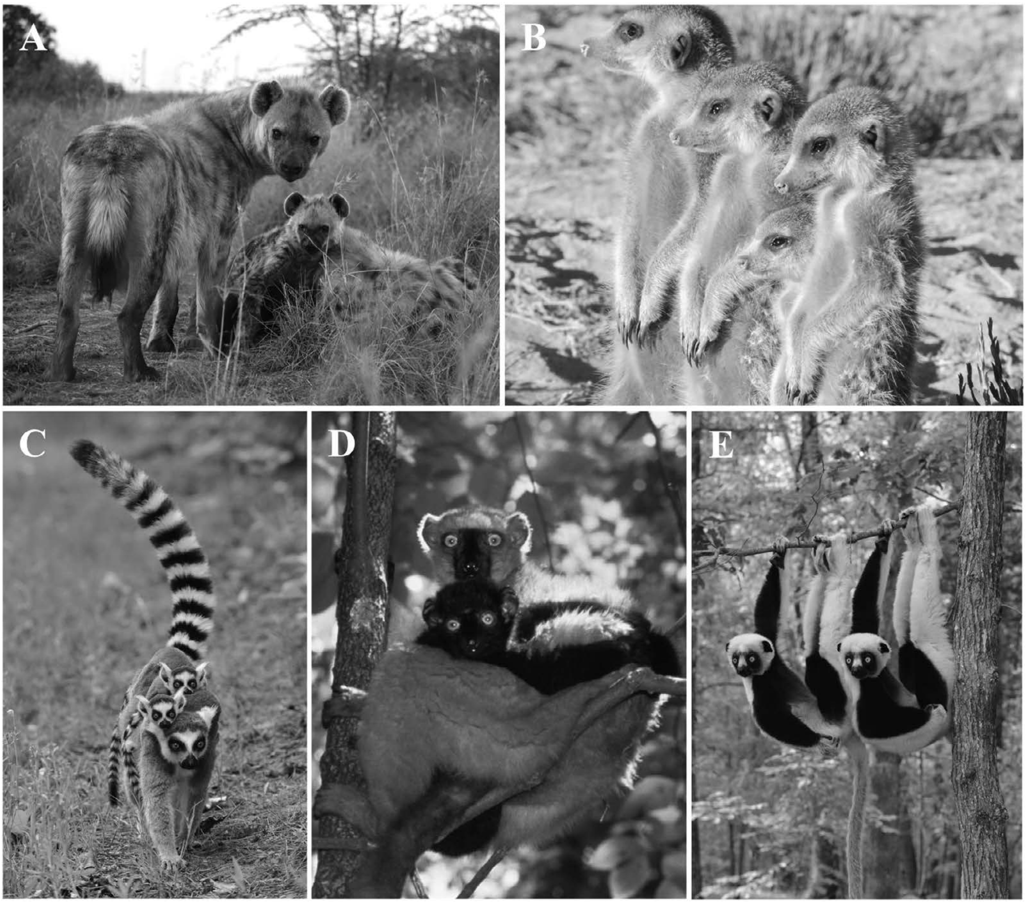

Figure 13.2 **'Experiments of Nature' for examining mechanisms of female aggression and social dominance**. Shown are social carnivorans, including (**A**) spotted hyenas (*Crocuta crocuta*) and (**B**) meerkats (*Suricata suricatta*), and strepsirrhine primates, including (**C**) ring-tailed lemurs (*Lemur catta*), (**D**) blue-eyed black lemurs (*Eulemur flavifrons*), and (**E**) Coquerel's sifakas (*Propithecus coquereli*), all of which show aggressively mediated female social dominance over male conspecifics.

Photos A–B provided by C.M. Drea; photos C–E provided by David Haring, Duke Lemur Center.

requires pre- or perinatal organization only, post-pubertal activation only, or a combination of the two. This framework has been validated by experiments that (1) block androgens or their actions in genetic males, producing 'feminized' males that show reduced aggression, or (2) increase exposure to progestins or androgens in genetic females, producing 'masculinized' females that show increased aggression—findings that are, respectively, paralleled in human syndromes, such as androgen insensitivity and congenital adrenal hyperplasia (Hines 1982).

Naturally 'masculinized' females

Endocrine patterns. The search for unusual androgen concentrations in socially dominant females has produced a range of findings, from limited peculiarities (Drea 2011), to rank-related patterns (Dloniak et al. 2006), to sex-reversed physiology (Koren et al. 2006; see also Figure 13.3). Initially focused on adrenal androgens, more recent attention has been accorded ovarian androgens: Androstenedione, originally considered a prohormone with no known androgen receptor, has been key to describing a placental route to exposing fetal females to maternal androgens (Glickman et al. 1992).

Species differences in absolute steroid concentrations generally have limited heuristic value for understanding hormone action, given the multiplicity of factors (e.g., carrier protein availability, receptor density, and distribution) involved in endocrine activation. Moreover, the typically exceptional status of female-dominant species within their genus limits the possibility for fruitful interspecies comparisons. Nevertheless, the *Eulemur* clade of strepsirrhine primates provides a unique opportunity to compare the behavioural endocrinology across several closely related species with differing intersexual and intrasexual aggression (Figure 13.3A): Within this clade, the females of female-dominant species show the predicted differences in neuroendocrine concentrations relative to their egalitarian counterparts. In other female-dominant species, androstenedione and testosterone concentrations also rise (alongside estrogen) during the breeding season (Figure 13.3B). Relative to males, some even display naturally high androgen concentrations year-round, (Figure 13.3C), especially during gestation (Figures 13.3C, D). Typically, elevations of androgen concentrations during pregnancy are modest or restricted to early gestation. By contrast, in these exceptional species, androgen concentrations peak in late-pregnancy, sometimes reaching or exceeding male values (Figures 13.3C, D). Third-trimester maternal androgens are particularly relevant to influencing the neural substrates underlying fetal behavioural differentiation (Licht et al. 1992; Drea et al. 2021).

Behavioural patterns. These endocrine patterns are matched in kind by female behavioural patterns, suggesting hormonal mediation of female aggression, dominance, and rough play (Figure 13.4). Within the *Eulemur* clade, the typical mammalian sex differences in aggression and dominance interactions are absent in egalitarian species and reversed in female-dominant species (Figure 13.4A). Within seasonally breeding, female-dominant species, female aggression increases more dramatically in the breeding season, relative to the nonbreeding season, than does male aggression, and is particularly directed toward other females (Figure 13.4B). These findings represent part of a burgeoning field of study that expands the Challenge Hypothesis to encompass female intrasexual competition and mating across vertebrates (Rosvall et al. 2020; Grebe et al. 2022).

Ontogenetic studies reveal an important null effect in exceptional females: the lack of sex differences in offspring aggression (Figure 13.4C). In mammals, one typically observes gradual development of male-biased aggression, whereas exceptional species can show early expression of aggression (Drea et al. 1996, 2021) and emergence of female dominance (Glickman et al. 1992; Grebe et al. 2019b). Lastly, experimental manipulation of androgen action in our focal species, via administration of an androgen receptor blocker (flutamide), significantly impacts concurrent adult behaviour in both sexes and, in pregnant females, the organization of offspring behaviour (Figure 13.4D). These maternal effects establish a mechanism for females to 'inherit' their mother's masculinized behavioural phenotype and potentially influence their reproductive trajectory (Drea et al. 2021).

Future Directions

Variability in the expression and mediation of aggression across species, sexes, and life-history stages calls for greater investigation of the mechanistic dynamics between underlying genetic, social, and environmental factors. Theoretical and technical advances in the study of behaviour have set the stage for integrative studies of aggression and social dominance at an unprecedented level of detail. Below, we highlight several promising avenues for research that integrate multiple, overlapping pathways for understanding the nature of aggression and social dominance.

Gonadal-independent mechanisms. Androgenic masculinization of brain development in sexual differentiation is unequivocal in vertebrates; nevertheless, recognition of the initial contribution of sex-chromosome factors calls for studies to investigate their interaction with gonadal hormones, whether

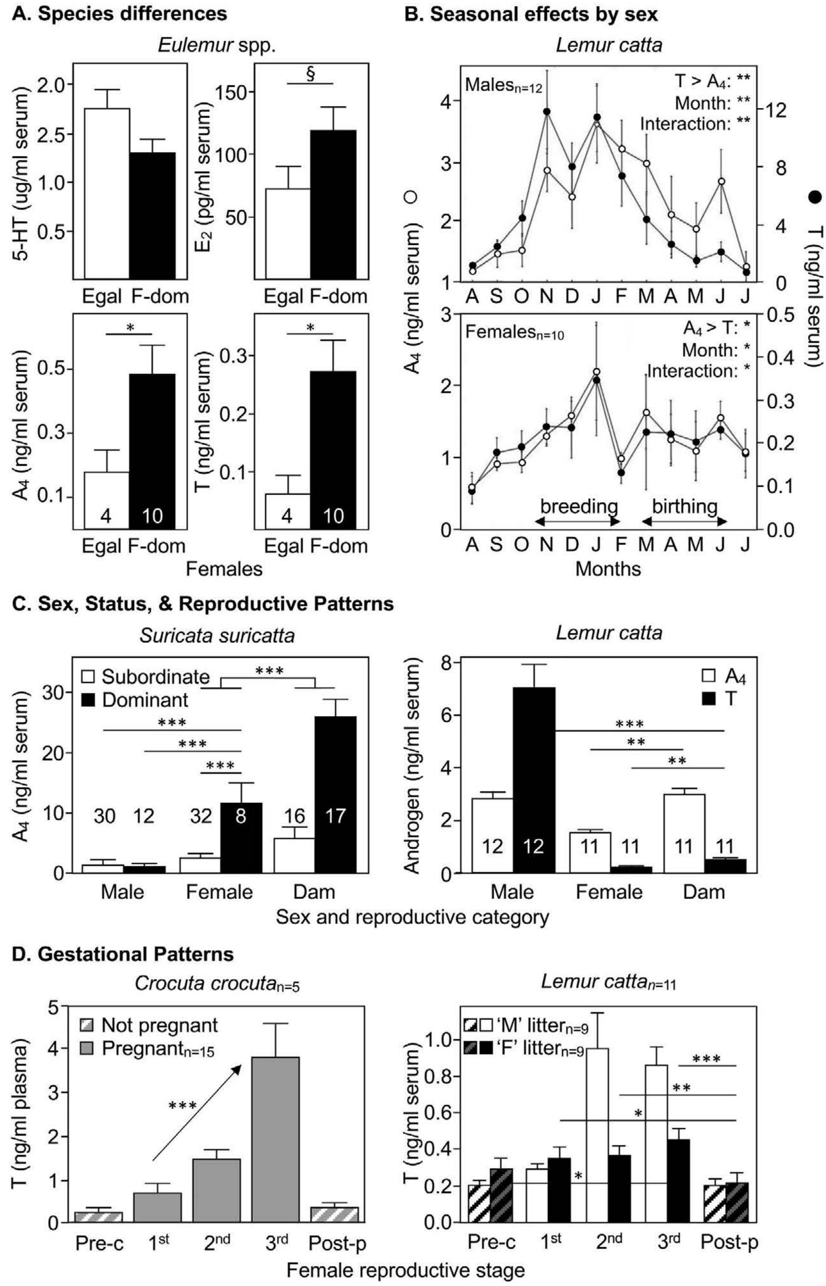

Figure 13.3 **Variation in serotonin (5-HT), estradiol (E2), androstenedione (A4) and/or testosterone (T) concentrations in 'Experiments of Nature.'** Shown (**A**) for females of closely related species, characterized as sexually egalitarian ('Egal': *Eulemur rufus, E. collaris*) or female-dominant ('F-dom': *E. rubriventer, E. flavifrons, E. coronatus, E. mongoz*; Petty and Drea 2015); (**B**) for *Lemur catta* from August–July in the Northern Hemisphere (Drea 2007); (**C**) by sex, social status and/or female reproductive state in *Suricata suricatta* (Davies et al. 2016) and *L. catta* (Drea 2011), and; (**D**) during pre-conception (Pre-c), first, second, and third trimesters, and post-partum (Post-p) in female *Crocuta crocuta* (Licht et al. 1992) and, also by fetal sex, in *L. catta* (Drea 2011).

Sample sizes shown; data adapted with permission; § $P < 0.10$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

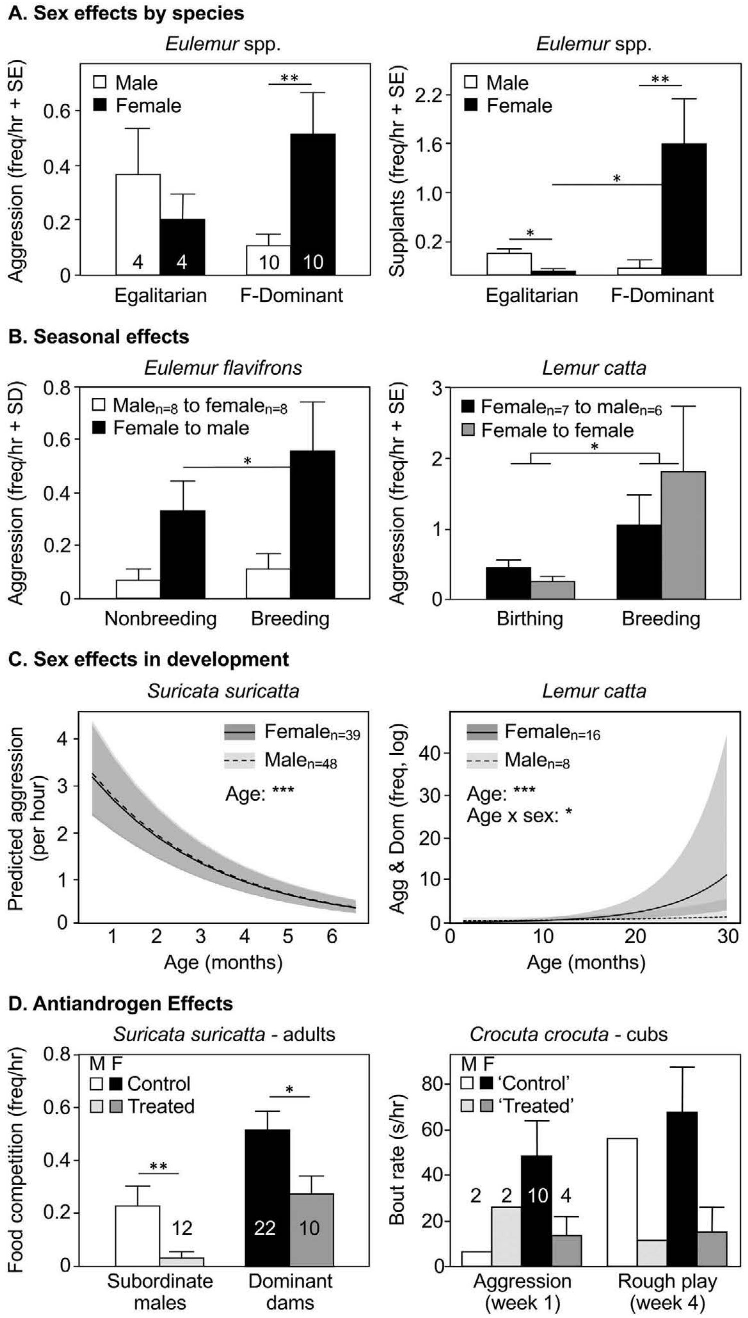

Figure 13.4 **Aggression, dominance, and rough play in 'Experiments of Nature.'** Shown are (**A**) rates by male versus female dyad members in closely related, egalitarian or female dominant *Eulemur* species (as in Figure 13.3A; Petty and Drea 2015); (**B**) seasonal rates within or between sexes in *E. flavifrons* (Grebe et al. 2022) and *Lemur catta* (Drea 2007); (**C**) predicted age-related rates by sex in *Suricata suricatta* (Drea et al. 2021) and *L. catta* (Grebe et al. 2019), and; (**D**) antiandrogen-modified rates by sex in adult *S. suricatta* (i.e., activational effects; delBarco-Trillo et al. 2016; Drea et al. 2021) and in the same-sex twins of treated *Crocuta crocuta* dams (i.e., organizational effects: Drea et al. unpublished data).

Sample sizes shown; data adapted with permission; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

in opposition or synergistically, to influence sex differences in the same phenotypes (Arnold 2020). In addition, Heimovics et al. (2015) review evidence across taxa for the rapid effects that neurosteroids, such as estradiol, have on aggression. Likewise, Munley et al. (2018) highlight the importance of the adrenal androgen dehydroepiandrosterone in certain rodent and avian species possessing a seasonal ‘switch’ from gonadal to adrenal regulation of aggression. Exploring paradigms such as these has the potential to greatly expand the realm of potential mediators of complex social behaviour.

Transcriptomics, gene regulation, and sociogenomics. The search for neuromolecular and genetic bases of aggression and dominance (Waltes et al. 2016) has benefitted from a new era of research in which genetic and epigenetic information are integrated with observation or manipulation of social environments to understand individual differences. Experimental and correlational work in primates shows that social stress from decreasing dominance rank alters control of the immune response via epigenetic plasticity (Anderson et al. 2020), providing a powerful link between an individual’s social environment and its physiology.

Social decision-making. Rather than aggression resulting from the independent activity of certain brain regions (several of which are reviewed above), a conserved system of brain structures and neurochemicals may integrate multisensory information to control a wide range of social behaviour, aggression included. Different social demands lead to alterations within this “Social Decision-Making Network” (O’Connell and Hofmann 2012), mediated by modulating neural gene expression. This idea has gained support, but key questions remain: One challenge is to identify network patterns specific to aggression. Here, comparative studies are crucial, as only certain animal models have allowed for distinguishing gene expression associated with status, rather than with reproductive physiology (Eastman et al. 2020).

Experimental studies and nonmodel systems. Numerous, well-established or cutting-edge experimental tools exist to manipulate endocrine function or receptor sensitivity, but they are typically applied under a limited set of conditions or to a limited array of species. There is thus a need for more widespread application of endocrine manipulations, particularly in natural settings (Drea et al. 2021), greater species breadth in examining hormone receptor distribution patterns and receptor function (Grebe et al. 2021), and the expansion to new study systems of technologies developed in model organisms.

Maternal, social, and transgenerational consequences. Differences in maternal traits or early-life experiences can have long-lasting effects on offspring behaviour, health, and fitness through a variety of causal routes. To tackle these multifaceted problems, future research on aggression and social dominance would benefit from (1) experimental and observational designs that allow for longitudinal examination and identification of multiple causal pathways; (2) more diverse biomarker sampling, especially within the brain, and (3) evolutionary, comparative methods that examine how different social systems produce different status-related gradients.

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14

MATING BEHAVIOUR

Patricia Adair Gowaty, PhD

Introduction

From a 50-year historical perspective six ideas organize scholarship about mating behaviour. The first is the modern renaissance of interest in Darwin's (1871) original idea of sexual selection (Box 14.1), which is a syllogism – an hypothesis – with assumptions, each of which should be evaluated scientifically before assuming that sexual selection has occurred. When each of the assumptions is met, one can infer that selection occurred; however, without test of its assumptions sexual selection always remains hypothetical. The second and third ideas from half a century ago – the anisogamy theory (AT) (Parker et al. 1972) and parental investment (PI) hypothesis (Trivers 1972) – each declared that intrinsic, inborn, physiological sex differences determine mating behaviour of "choosy, coy females" and "indiscriminate, profligate males". The fourth resides in experiments designed to test the veracity of the predictions from PI and AT. It is not enough that a theory makes "reasonable" predictions, what's essential are experimental tests of theory: tests that go beyond confirming expectations, such as those that evaluate alternative predictions. Are females ever indiscriminate? Are males ever coy? Do the sexes behave as theory predicted? Is behaviour of females and males similar under similar ecological and social conditions? The experiments discussed herein reject the expectations of intrinsic, inborn sex-biased differences in reproductive decision-making. The alternative perspective says "in reproductive decision-making there is nothing so like a female as a male and *vice versa*". That is, individuals often express "adaptive flexibility in reproductive behaviour", a kind of developmental, probably epigenetically organized phenotypic plasticity (Ah-King & Gowaty 2015, 2016). The fifth describes how parents compensate (Gowaty 2008) for offspring viability deficits when they are coerced into mating with partners they do not prefer. The sixth is a sex-neutral idea, the Switch Point Theorem – SPT of Gowaty & Hubbell (2009) that mathematically proves that individuals independent of their sexes make reproductive decisions – whom to mate and whom to reject as a potential mate – based on similar ecological and social constraints and opportunities in the environments individuals experience. A corollary of the SPT is the "killing time hypothesis" (Gowaty & Hubbell 2010) that solves the conundrum of why individuals ever hurt their mates.

Sexual Selection

Charles Darwin's (1871) ideas about sexual selection (Box 14.1) codified courtship and same-sex combat over access to potential mates as mechanisms of reproductive decision-making, whereby one or both sexes sport display traits, such as fancy feathers and large antlers, that catch the attention of

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opposite sex individuals, who then evaluate the attractiveness or fitness of opposite sex alternative potential mates – supposedly because of the "display" traits. Such courtship is highly variable across and within taxa. The modalities of courtship include fancy and or dramatic visual signals, dances, calls, songs, and olfactory signaling.

Box 14.1 Sexual Selection is Always an Hypothesis until Empirically Proven

Sexual selection is a type of natural selection, *i.e.,* not artificial selection as practiced by animal breeders. As in all selection hypotheses, sexual selection has three assumptions that must be met to demonstrate that sexual selection occurred. The first is about the units or *"level" of selection:* in sexual selection units are sex specific, *i.e.,* sexual selection among females depends on the existence of genetically heritable as well as phenotypic plastic trait variation of available females, while sexual selection acting on males depends on the existence of genetically heritable and phenotypically plastic trait variation among available males. The second assumption is about the *"mechanisms" of selection* that sort among the trait variants among the units of selection. In sexual selection the main mechanisms are between-sex mate choices and within-sex competitive interactions over access to mates. The third and most important assumption is about *the fitness rewards* that accrue to the units of selection (either females or males) because of the effect on the traits of individuals that are affected or not by the exertion of the mechanisms of selection. Proving that sexual selection occurred depends on demonstrating the veracity of the most important assumptions: namely, how do individuals behave and what are the fitness consequences of their behaviour? Without reliable evidence that these last two assumptions are met, saying that selection has occurred is misguided. Therefore, we must always be skeptical about sexual selection unless experimental or reliable observational evidence exists about mechanisms of mate choice or same-sex competition. And, we must pay attention to the most important aspect of sexual selection: the evaluation of fitness variation among potential mates and rivals.

Darwin (1871) speculated men chose women as mates: he opined that male choice accounted for the evolution of attractiveness of women. So it is not a surprise that the first experimental studies of mate choice evaluated males' choices of females (in Drosophila flies). Yet, for a very long time and especially after 1972, typical expectations about how sexual selection worked focused on female choice of males' display traits, and the competitive interactions of male rivals, usually leaving out evaluations of male choice of females' display traits or the possibility of competitive interactions of female rivals. Most early tests were about behaviour without measurement of fitness outcomes of an individual's mate choice or the outcomes of competitive interactions among rivals.

Anisogamy Theory and Parental Investment

In 1972 two theories appeared each concluding that females were most likely to be choosy and males most likely to be indiscriminate about whom they mated, sometimes also competing with male rivals over access to females. Geoff Parker et al. (1972) argued that gamete size variation (anisogamy) determined which sex was choosy and which competitive. Trivers (1972) argued that parental investment differences between the sexes determined which sex was choosy and which indiscriminate. The reasoning of Parker et al. (1972) was based on the math of gamete encounters when some were small and vagile (as in sperm) while others were large and sedentary (as in eggs). Encounter probabilities of females' and males' gametes suggested large, resource rich females with large relatively sedentary gametes would evolve to be choosy, while resource poor but vagile males with small gametes would evolve to be indiscriminate. Trivers' idea was based on the usual high investment in gestation and lactation of mammal females compared to the negligible parenting contributions required from mammal fathers, thus he reasoned that females evolved to be choosy, while males evolved to be indiscriminate. These theories seemed so true that a type of scientific deception called theory tenacity set in: that is, the theories persisted in the minds of some scientists despite considerable contrary evidence (Loehle, 1987, p. 397) showing that males were sometimes choosy and females sometimes indiscriminate.

The hypotheses of Parker and Trivers not only canalized expected behaviour of females and males, but re-ignited interest in the then all-but-forgotten paper by A. J. Bateman (1948) that codified profound sex differences in reproductive decision-making that was said to determine sex differences in variances in number of mates (NM) and variances in number of offspring, called reproductive success (RS). Bateman said that the variances in NM and RS of males was greater than the variances in NM and RS of females, which implied that "evolutionary potential" was greater among males than among females. "Evolutionary potential" refers to standing variation among individuals in a population: the greater the genetic variation among individuals, the greater trait variation likely exists among individuals, an argument that some scientists have used to claim that males are more influential to evolutionary change than females (Trivers 1972). AJB concluded without observational evidence that the sex differences in variance in NM and RS were because females were "coy" and males were "competitive". But AJB's conclusions lacked experimental rigor as Snyder & Gowaty (2007) first demonstrated, and as Gowaty, Kim & Anderson (2012) verified with a large repetition of AJB's methods. A subsequent series of monogamous control experiments (Gowaty, Kim, & Anderson (2013)) further buttressed observations of errors in Bateman's iconic study. Hoquet, Bridges & Gowaty (2020) then debunked Bateman (1948) with thorough analysis of AJB's hand-written lab note data. Reanalysis demonstrated Bateman's hand-written data failed to support his published conclusions, or "Bateman's Principles" (Arnold 1994).

So what were the mistakes that Bateman (1948) made? The first error he made was associated with his method of identifying which offspring came from which parents. To uniquely identify parental success, he used extreme phenotypically obvious inherited mutations in the offspring. The parental mutations were dramatic and in some cases homozygous lethal, so it was no surprise that offspring inheriting two different and dramatic parental mutations often died before eclosion and thus did not occur in the expected frequencies for the four types of expected offspring, thereby creating a bias in accounts of reproductive success in parents. Second, there was no evidence in Bateman's paper that he had actually observed the behaviour of the flies in his 65 populations, meaning that careful readers realized that Bateman's conclusions of sex-related behaviour were inferred rather than observed. Third, he pseudoreplicated his analyses combining individuals from different populations, thus violating the sexual selection tenets that hold that in order for individuals to choose among potential mates or to compete with same sex rivals, they must be in the same population! That Bateman's paper remains among the most cited papers in sexual selection says that many readers fell for biological (sexual) essentialism, gender biases associated with "true belief" and confirmation biases (Loehle 1987). The problems in Bateman's original analysis of his data are profound and beyond the limits of this chapter, but five published papers discuss the breadth and the width of Bateman's errors (Snyder & Gowaty 2007; Gowaty et al. 2012; Gowaty, Kim, & Anderson 2013; Gowaty 2018; Hoquet, Bridges, & Gowaty 2020).

Experimental Challenges

Experimental tests of fitness outcomes in relation to parental investment and anisogamy are rare. But, some experiments testing the veracity of parental investment and anisogamy predictions of sex differences and fitness outcomes do exist. Courtship studies usually evaluate females' choice of males, as a function of specific observable, phenotypically discernable variable traits in males, often without similar attention to males' choices of variable traits in females. What seems to fascinate most investigators is the question "what is attractive", while leaving unevaluated the fitness consequences of choices by either sex. Recent text books – *Mate Choice* by Gil G. Rosenthal and *A Taste for the Beautiful: The Evolution of Attraction* by Michael J Ryan – described the two most frequently evaluated assumptions of sexual selection hypotheses: mate choice in one sex related to phenotypic variation in the opposite sex and same-sex competitive interactions. Both books describe considerable accomplishments in the study of sexual selection detailing descriptions of evaluation of two of the assumptions of sexual selection via mate choice. Yet, each author left un-explored the most important assumption of any sexual selection hypothesis: *i.e.*, the fitness consequences. The fitness measures that usually engage evolutionary biologists include an individual's number of mates, their number of offspring, and the viability of offspring. Offspring viability is perhaps the most important fitness measure, because it is a predictor of lineage success. It is usually calculated as a given female's fraction of eggs that live to adulthood. Offspring viability is the key measure of fitness for females. (It may be important in males, but typically it is harder to measure sperm-to-adult survival.) Experiments described below using flies, mice, and ducks were designed to evaluate sexual selection's assumptions about fitness particularly in relation to whether an individual mated with a partner they preferred or with a partner they did not prefer.

Experiments Matter

In the first day of my first class as a graduate student my instructor emphasized the importance of "strong inference experiments" (Platt 1964). "Strong inference" consists of devising alternative hypotheses; organizing a "crucial experiment" performed with rigor, so that alternative possible outcomes can exclude one or more of the hypotheses. That lessen initiated my abiding interest in some of the world's great experimentalists cited below.

> *"The human understanding is no dry light, but receives infusions from the will and affections; whence proceed sciences which may be called 'sciences as one would'. For what a man had rather were true he more readily believes. Therefore he rejects difficult things from impatience of research; sober things, because they narrow hope; the deeper things of nature, from superstition; the light of experience, from arrogance and pride; things not commonly believed, out of deference to the opinion of the vulgar. Numberless in short are the ways, and sometimes imperceptible, in which the affections color and infect the understanding."*
>
> *Francis Bacon, Novum Organon (1620).*

"*Science is a way of trying not to fool yourself. The first principle is that you must not fool yourself, and you are the easiest person to fool*" (Richard Feynman: date unknown). In that vein a type of self-deception or "true belief" is "confirmation bias", sometimes called "theory tenacity": the "persistent belief in a theory despite contrary evidence" (Loehle, 1987, p. 397), which can sometimes seriously misguide scientists studying gender because of typical society-wide double standards associated with being female and male (Gowaty 2018).

FLY EXPERIMENTS

Mutual Interest Between the Sexes!

Investigators tested whether the pre-mating behaviour of female *Drosophila pseudoobscura* was passive and "coy" relative to more active, "ardent'," and indiscriminate males, as well as if males were sometimes passive and "coy". Using virgins, experimentalists (Gowaty, Steinichen, & Anderson (2002)) focused on females' approaches to males of *D. pseudoobscura* prior to courtship and copulation: were females "ardent"? Did *D. pseudoobscura* males resist female approaches: were males "coy"? Video records captured individuals' movements and interactions with other conspecifics, unexpectedly showing that females approached males as often as males approached females, while equally unexpectedly males avoided females as often as females avoided males. The videos showed that females willing to mate are often extremely still, a "come on" to a male! In this experiment, the total number of offspring emerging as adults correlated with mutual, pre-courtship interest of female and male flies, a result inconsistent with parental investment and anisogamy predictions. The investigators speculated that in nature females may commonly approach males soliciting courtship, perhaps as often as males solicit females.

Gamete sizes failed to predict reproductive behaviour of females and males!

Three species of *Drosophila* with profound differences in female to male gamete sizes facilitated a test of parental investment predictions. *D. hydei* have very large sperm; *D. pseudoobscura* have among the smallest of sperm within the genus Drosophila. *D. melanogaster* have typical sized sperm for the genus. Parental investment theory and anisogamy theory predict that *D. hydei* males and females are equally likely to be coy, while *D. pseudoobscura* and *D. melanogaster* males are likely indiscriminate while females are likely coy. Observations showed: *D hydei* were not sex-role stereotyped because both females and males were "coy". In contrast *D. pseudoobscura* and *D. melanogaster* females were often coy and males often indiscriminate, demonstrating expected sex roles. However, *D. pseudoobscura* females approached males more often than *D. melanogaster* females did, and male *D. hydei* approached females as often as males of the other two species, both results inconsistent with parental investment theory. Male *D. pseudoobscura* and *D. hydei* were more likely to approach males in same-sex pairs than male *D. melanogaster*. Drosophila species with sex differences in gamete sizes failed to match parental investments or anisogamy's expected sex differences in behaviour (Gowaty, Steinichen, & Anderson 2003).

Social constraints on mate preferences decreased offspring viability and fitness of mated pairs

Anderson, Kim, & Gowaty (2007) tested the hypothesis that social and ecological constraints – bad luck, bad weather, few potential mates – affect the fitness outcomes from a mating. In this experiment *Drosophila pseudoobscura* females and males made mate choices that the investigators studied in order to find out the fitness effects on the viability of offspring when an individual was paired with an opposite sex partner they preferred or did not prefer. Novel mate preference arenas eliminated same-sex conflict as well as opposite-sex coercion of subjects, but allowed observers to measure the time that a subject fly was nearest to one of the opposite-sex target flies in their arena. Investigators assumed that subjects that spent more time nearest to one potential mate than the other in a mate choice arena was their preferred opposite-sex partner. The "constrained subjects" were allowed to mate only with their non-preferred (NP) partners, while "unconstrained subjects" were allowed to mate with their preferred (P) partners. *D. pseudoobscura* females and males that were constrained to mate with their NP partners had fewer offspring of lower viability than subjects that were unconstrained and able to mate with their P partners.

Mating opportunities affect female fitness!

In nature, mating opportunities are often stochastic. Unlucky individuals might never mate, others may mate only once, some may live in lifelong monogamy, while others may mate with many different individuals over a lifetime, some with opposite-sex virgins, and some with opposite-sex partners mating every day. To understand how fitness varied under different mating opportunities over female lifetimes Gowaty et al. (2010) used female *D. pseudoobscura* in three different treatments (females with one copulation, females mated every day to the same male, and polyandrous females mating each day with a novel male), to evaluate how mating opportunities affected mother longevity and offspring viability. Later, Castrezana, Bridges, & Gowaty (2017) organized a large study using *D. melanogaster* with five treatments. These were: (1) lifelong female virgins never exposed to males, (2) females mated once in their lives (on the first day of the experiment), (3) monogamous females lived with the same male and mated him throughout life *ad libitum*, (4) females exposed each day to a novel young virgin male each day of life, so that over their lives females mated polyandrously, and (5) females exposed to a novel experienced male the same age as the female, on each day of life, so females mated polyandrously. Results: compared to lifelong virgins, once-mated females had enhanced survival. Multiple copulations increased offspring numbers for monogamous and polyandrous females. Compared to monogamous females polyandrous females mating daily with new age-matched, experienced males had longer living offspring than monogamous females. Females mated to novel virgin males had shorter lives than females mated with age-matched males. Stochastic mating opportunities affected female fly fitness. These experiments revealed females' opportunities to mate have profound effects on female lifespan and the number of offspring produced. More experiments like these will inform further the opportunities and constraints of females in nature. Note that these experiments on flies are easily done, while similar experiments on say, red deer (*Cervus elaphus*) or eastern bluebirds (*Sialia sialis*), are likely impossible.

MOUSE EXPERIMENTS

Mate preferences influence females' fitness

An early experimental test of the expectation that mammal females mating with males they prefer produce longer lived, more viable offspring than females that mate with males they do not prefer showed that offspring viability, a predictor of lifespan, was statistically greater when female mice mated with their P males rather than their NP males. Females mated to their P males had more litters with offspring exhibiting enhanced performance in dominance contests and nest building. Furthermore, females mated to P males had offspring of higher viability than females mated to NP males (Drickamer, Gowaty, & Holmes 2000). Females able to act on mating preferences free of social and ecological constraints accrued viability benefits for their offspring. These observations are consistent with Altmann's (1997) hypothesis that offspring viability, calculated as the ratio of number of eggs laid and surviving to reproductive age, is a key measure of mothers' fitness and lineage success.

Mate preferences influence males' fitness in mice

The first experiment (Gowaty, Drickamer, & Schmid-Holmes 2003) in a mammal of fitness benefits of male choice behaviour used feral house mice (*Mus domesticus*) to evaluate if male mate preferences influenced their fitness. The experimentalists controlled female preferences, same-sex competitive interactions, and phenotypic traits that could have influenced males' mate choices. Half the males were placed to breed with their P females, half with their NP females. Males mated with their P females sired more litters than males mated with their NP females. Offspring viability was significantly lower when males reproduced with their NP females than when they reproduced with their P females. Adult sons of males that mated with P females were socially dominant to sons of males mated with NP females. Adult offspring from P pairings built better nests than offspring from NP pairings. The slope of the survivorship curve for P offspring was significantly higher than for NP offspring. Male mate discrimination influenced offspring health, lifespan, competency in nest building, and dominance behaviour of sons, all results inconsistent with PI and AT predictions, as well as Bateman's principle that males are indiscriminate. *Mus* male mate choice mattered!

Fitness under mutual mate choice preferences in mice

Drickamer, Gowaty, & Wagner (2003) evaluated fitness in mice under mutual choice of female and male partners, revealing consistent differences between mating pairs in which each preferred the other (P–P) versus when each did not prefer the other (NP–NP). The number of pups weaned, their time to first litter, their birth-to-weaning viability, and pup body weight at birth and weaning, as well as the growth rates for pups of both sexes were consistently greater for progeny from P–P matings than NP–NP matings. P–P progeny displayed behaviour indicating higher fitness more often than progeny from NP-NP matings. When social constraints on mutual mate preferences were relaxed in each sex, breeders produced highly competent progeny, with high viability. The more subjects preferred each other, the greater the viability and performance of their offspring, a conclusion again inconsistent with PI and AT.

DUCK EXPERIMENTS

Mallard females' mate preferences affect mothers' fitnesses

Males sometimes force-mate females, as happens in the notorious coercive mating in mallard ducks (Gowaty and Buschhaus, 1998). Constraints theory (Gowaty 2008) predicted that females reproducing under coercion would produce lower viability offspring than females reproducing without coercion. Using mate preference trials, Bluhm & Gowaty (2004a) placed wild female mallards to breed with their P or NP partner and then evaluated female fitness components (egg number, number of offspring alive at 45 days post-hatch). Mothers paired with their NP partners had statistically fewer offspring than mothers paired with their P partners. Between-female variation in productivity (% living offspring) showed that females' ability to avoid social constraints such as forced matings with NP males accrued large positive effects on their fitness. The study remains one of the few showing fitness deficits for offspring and mothers under enforced, often coercive, reproduction with NP males. It emphasized the curious behaviour of males who hurt their prospective or actual mates, raising the question of why individuals ever hurt a potential mate, a topic discussed below in the context of the "killing time hypothesis".

Coerced mallard females make up for offspring viability deficits

The compensation hypothesis (Gowaty 2008) predicted that constrained females – those coerced to mate with NP males – have lower viability offspring, compelling mothers to enhance resources directed to those lower viability offspring. Female mallards breeding with males they did not prefer enhanced the mass of their eggs as well as the number of their eggs, increasing the likelihood that some of their offspring survived to fledging (Bluhm & Gowaty 2004b). Directing maternal resources to vulnerable offspring also implies that mother's survival is also potentially at risk, suggesting that attention to the costs of coerced mothers' survivorship deserves much more attention from animal behaviourists.

PHENOTYPIC PLASTICITY EXPERIMENTS

Sex as a reaction norm

Ah-King & Gowaty (2015) joined a worldwide discussion of sexual selection theory focused on sex differences by emphasizing that sexed traits of humans are frequently continuously variable arising via developmental reaction norms under genetical, epigenetical, social, ecological, and environmental inducers of gene expression. They emphasized: “there is nothing so like a female as a male and *vice versa*”. Later, Ah-King & Gowaty (2016) reviewed published experiments using non-human animals designed to evaluate how environmental circumstances affected choosers’ behaviour and choosers’ traits. They found 3000 studies of phenotypic plasticity: 198 described experiments of within-sex phenotypic plasticity in mate choice flexibility: 16 had no evidence of mate choice flexibility, but 182 studies described subjects changing their mate choice behaviour. The investigators of these 182 studies attributed subjects’ changes in behaviour to adult sex ratios, operational sex ratios, potential reproductive rates, predation risks, disease risks, chooser’s previous mating experiences, choosers’ ages, chooser’s condition, or chooser’s resources, revealing a plethora of ecological and social reasons that induced their subjects to change from choosy to indiscriminate or indiscriminate to choosy. Choosers’ choosiness was socially labile, due to their *ecological/social circumstances*, not due to their intrinsic, inborn sex! The 2016 review revealed that choosiness is very often “environmentally induced”, *i.e.*, not fixed in “the choosy sex”. Contrary to expectations from PI and AT, the 2016 result demonstrated that the characteristics of potential mates had little to do with the subjects’ mate choices. Rather, characteristics of female and male choosers and their ecological circumstances mattered more to their mate choice decisions than the traits of potential mates! The data from the 2016 review fundamentally challenged claims of universally choosy females and universally indiscriminate males. A curiosity was that in none of the 182 studies did the original authors note that the behaviour of their subjects failed to meet expectations of intrinsic inborn sex-specific behaviour predicted by PI and AT.

What did our experiments above reveal?

First, mate choice by either sex has profound effects on parental fitness relative to the health and viability of offspring. Second, environmental and social opportunities and constraints on mating opportunities have powerful influences on fitness outcomes for individuals: that is, the intrinsic characteristics of individuals did not determine fitness outcomes. What mattered were the social and ecological opportunities that the subjects were dealt. Third, the science of sex-differentiated behaviour is in need of a makeover, a re-evaluation of the origins and degree of sex differences in courtship and mating behaviour. Our experiments showed that similarities between the sexes are common. Most notably, our experiments indicated that what individuals do has little to do with the costs of parental care, sizes of their gametes, their traits, or their intrinsic characteristics. Rather, what mattered in these experiments was the ecological or social circumstances of subjects. What mattered was whether an individual preferred a given potential mate or not.

Thus, a modern question is how different are the sexes in reproductive decision-making? What might we be missing when we fail to consider that females and males might not be all that different when it comes to reproductive decision-making? Could it be that the politics of misogyny and sexism maintain and organize continuing unrealistic notions of biological and ecological sex differences in reproductive decision-making that then promote gender dynamics that obscure the considerable similarities of individuals of different sexes (Gowaty 1992)? The next section is about a new theory of mating positing that in reproductive decision-making there is “nothing so like a female as a male and *vice versa*”.

Time, Chance, and Mate Choice

The Switch Point Theorem (SPT) is a novel mathematical statement, an hypothesis, showing that stochastic effects on an individual’s probabilities of survival, mate encounters, and durations of their latencies to further mating determine an individual’s time available for mating, and ultimately the mean and variance in their fitness (Gowaty & Hubbell 2009). These probabilities favor individuals able to make adaptively flexible reproductive decisions independently of competitive interactions with same sex rivals. What makes it different from earlier ideas are that the forces driving individuals' reproductive decisions are not about intrinsic, inborn characteristics, but environmental and social conditions *experienced by individuals*. The SPT is a considerable departure from past animal behaviourists' expectations about reproductive decision-making.

Two novel ideas inspired the SPT. First Bill Sutherland's (1985) paper showed that rather than competitive interactions among males and choosiness of females, chance explains Bateman's (1948) results. Sutherland's model showed Bateman's results were due to stochastic effects rather than intrinsic behaviour of subjects. His idea was non-intuitive, challenging the sexual selection hypothesis. His paper inspired Hubbell and Johnson (1987) to study how chance operates to affect reproductive decisions and lifetime fitness. Their math exposed that determinants of reproductive decisions came from individuals *independent of their sex*, organized not by intrinsic sex differences, but by ecological-social constraints and opportunities that individuals experienced.

The Thing that Matters is Time

The Switch Point Theorem (SPT) (Gowaty & Hubbell 2009) is a quantitative statement of an hypothesis that in life, "time is everything". Chance effects on an *individual's survival*, her or his *encounter probabilities with potential mates*, and *the duration of latency to further mating after a mating* affect an individual's time available for mating, reproduction, and reproductive success. The SPT is a departure from the usual discussions of reproductive decision-making, *i.e.*, it does not depend on trait variation in potential mates, or within-sex competitive interactions with rivals, nor on their gamete sizes, nor on their parental investments. The thing that matters in the SPT is time! How much time an individual has left in life matters, numbers of encounters with potential mates matters, and an individual's accumulation of lifetime reproductive success matters, all of which depends on the population distribution of fitness and ultimately on lifetime reproductive success of an individual's descendants (Gowaty & Hubbell 2009).

The SPT is a quantitative alternative to the qualitative ideas in sexual selection. It is derived from an absorbing Markov model predicting an individual's reproductive decisions given variation in the individual's social and ecological environments. In the SPT what matters is the time an individual spends in each of four states. At sexual maturity an individual enters a receptive-to-mating state. After encountering potential mates, an individual can enter a state of mating any encountered potential mate (being "indiscriminate") or it can wait for a better mate (being "choosy"). If it mates, it may enter a period of "post-mating time out" or "latency", lasting a few seconds or infinitely. And from any of the previous states an individual can enter an "absorbing state", otherwise known as "death".

Two probabilities determine the movement of an individual from state to state: the individual's survival probability, s, and its probability of encountering potential mates, e. With these two probabilities we can calculate an individual's expected lifetime mating success. Add more complexity and one can predict the effects on expected lifetime fitness from mating with any of the n (number of) potential mates in a population by assuming an individual will uniquely rank all potential mates in a population from 1 (best for them) to n (worst for them). The switch point sorts potential mates into "unacceptable" or "acceptable" for the target individual. The dividing line along the axis of ranked potential mates is the high point of the curve of fitness reward for a given switch point. The math exposes the switch point that maximizes fitness by comparison of all possible switch points along an axis of ranked potential mates. So, say for $n = 100$, the switch point that maximizes fitness, $f^{\star}$, could be between potential mates ranked, say, 1 and 2, or say, 30 and 31, or say, 70 and 71, or even 99 and 100, etc.

The best way to master the SPT is to become familiar with its elements. The online "SPT toy" (http://shiny.eeb.ucla.edu/switch-point-theorem/) (La Rosa & Gowaty 2018) is something one can play with to learn how the SPT works. The SPT toy allows players to deduce its predictions by

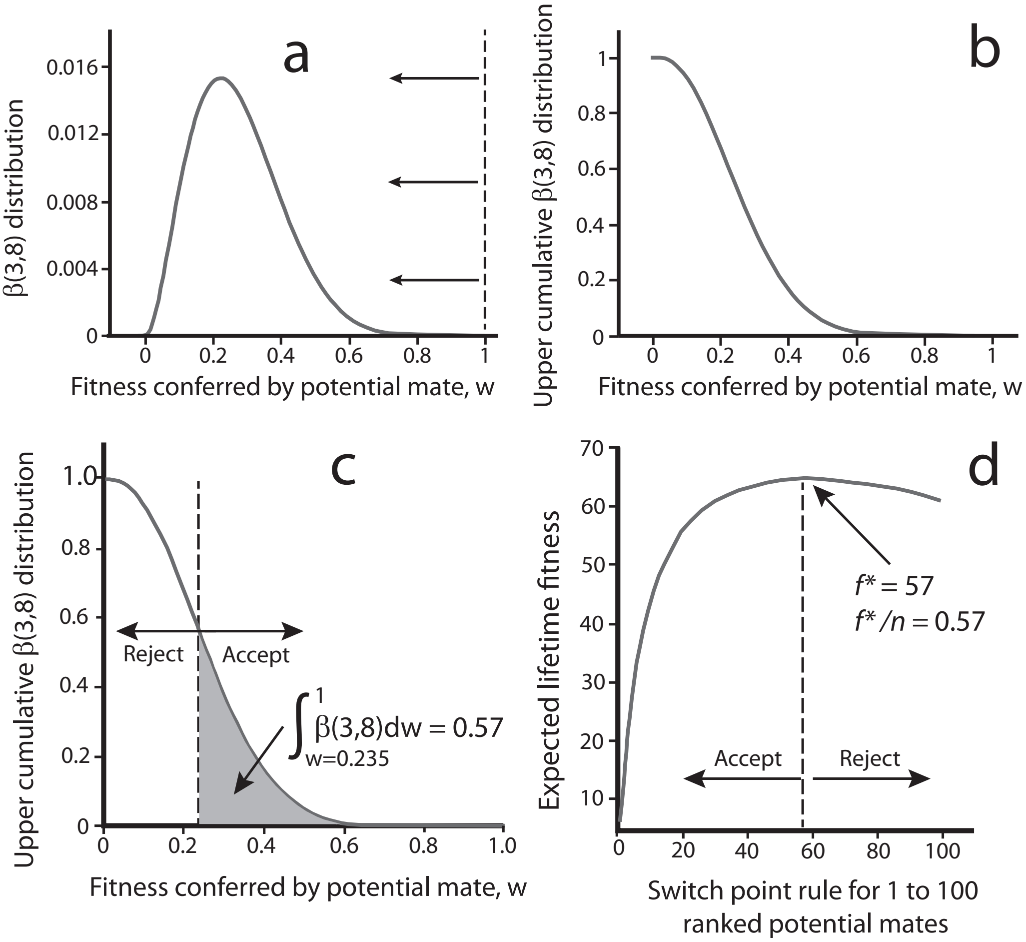

Figure 14.1 Example of a calculation of the switch point mating decision rule for a focal individual having 100 potential mates in which the distribution of fitness conferred is β(3,8). The focal individual has an encounter probability of $e = 1$, a survival probability of $s = 0.999$, and a timeout $o = 2$. Panel a: the *w*- distribution β(3, 8). Panel b: the upper cumulative distribution of β(3, 8). The upper cumulative distribution is obtained from the area under the beta distribution curve in Panel *a*, obtained as the area under the beta distribution curve to the right of the vertical line with 3 arrows moving from right to left. Panel c: the definite integral of potential mate fitnesses that are acceptable (shaded area). Panel d: expected lifetime fitness as a function of the switch point rule (*f*). The maximum occurs when 57 of the 100 available potential mates are acceptable ($f^{\star}= 57$). From P. A. Gowaty and S.P. Hubbell (2009).

toggling parameters. Stochastic model parameters, as well as their number, make teaching the SPT a bit challenging, so I advise readers to play for a while! One can use the toy's text to see how the parameters change as the equation's solution $f^{\star}$ changes. Changes in each parameter result in unique and sometimes surprising changes to $f^{\star}$, which is the value that toggles the dividing line between the individual's ranked acceptable and unacceptable potential mates.

What one finds as one increases understanding of the SPT is that it proves theoretically that individuals can enhance their average lifetime fitness by flexible reproductive decision-making. It suggests a new program of research focusing on ecological and social conditions in the experiences of individuals that then organize what they do: intrinsic inborn differences may matter far less than an individual's social and ecological environments.

The Killing Time Hypothesis: A Mechanism of Sexual Conflict

The killing time hypothesis (KTH) (Gowaty & Hubbell 2010) is a corollary to the SPT. The key parameter in the SPT is how much time an individual has left in life, *i.e*, their survival probability, which means that individuals with low survival probability will settle for lower quality mates, so it is no surprise that under sexual conflict (Gowaty 2017) mechanisms for increasing a chooser's willingness to accept lower quality mates have evolved, and yes, the mechanisms of killing time are not pretty. The KTH says that a previously rejected individual can increase the odds that a previously resistive potential mate will turn around and accept them, if the rejected potential mate lowers the survival probability of the resistive potential mate. A rejected potential mate could change a previously resistive potential mate into a willing potential mate by hurting them in ways that reduce their instantaneous survival probability. Draconian? Yes! Nevertheless, hurting a potential mate is more "effective" than many of us would like to imagine. For example, a recent study found that women who suffered forced copulation are more likely to become pregnant than women who engaged in consensual sex (J. A. Gottschall & T. A. Gottschall, 2002, *Human Nature*, vol. 14, #1, pp. 1–20).

When the fitness interests of potentially or actually mating individuals are opposed, the opportunity for sexual conflict exists (Gowaty 2017), and fitness outcomes from conflicted matings are low viability offspring as indicated by the experiments in flies, mice, and ducks above. Evolutionary theory says sexual conflict is an inevitable by-product of coercive males and vulnerable females (but females can be coercive and males vulnerable). Sexual coercion, like forced copulation, inspired discussions of female resistance to male attempts to control female sexuality in ducks, flies, mice, and humans. Resistance theory (Gowaty & Buschhaus 1998) focused on variation among females positing that selection acts on females to resist male attempts to control their behavioural or physiological reproductive decisions or to otherwise attempt to make up for fitness losses. Resistance theory predicts that environmental variation allows parents and prospective parents to up-regulate compensatory behaviour (Gowaty 2008), enhancing lifespan of otherwise low viability offspring, but likely at a cost to the longevity of mothers.

Without SPT parameters, it is hard to understand how hurting a potential mate would increase the likelihood that she or he would mate the aggressor, but interesting in the context of the behaviour of non-human animals in which the time available to females for reproduction and further life is commonly used up by the machinations of males holding on to females (Darwin 1871). As I recounted (Gowaty & Hubbell 2010), Darwin (1871) was mystified in his attempts to understand curious traits restricted to males but not used in competition with rivals. These included organs to "seize females once found" or to "prevent her escape", the use of traumatic attachments to females of male tentacles via the sucker discs of cephalopods, the modified antenna of lower crustaceans into an "elegant, and sometimes wonderfully complex, prehensile organ" (Darwin 1871, p. 330), the pincers of some males that they use to "seize with impunity" females before they have molted their hard shells, before they were ready to mate (p. 331). Darwin put organs for catching, seizing, restraining, holding, and preventing the escape of females aside as unlikely due to advantage acquired over rivals, even though these organs were seemingly important to gamete transfer, and even though similar organs were most often absent in females (but see Darwin 1871, p. 332). Could it be that the "difficulty in the act" (Darwin 1871, p. 332) that worried Darwin, was a mechanism by which males reduce the survival probabilities of females making those females more likely to mate with the aggressor, whom she would otherwise reject if her survival probability had not been compromised? Lowering a female's survival probability gives reproductive advantage to coercive males. Keep in mind: as the experiments described throughout this chapter showed, producing highly viable offspring is greatest when individuals prefer each other. So, what we need now are experiments that expose ways that females (and males) resist coercion. It is worth noting: "making time" mechanisms increase a potential mate's likelihood of survival, long life, and offspring viability. "Killing time" is dramatic. "Making time" less so. "Making time" is unexplored territory: an opportunity for new experimentalists to make their names in animal behaviour!

Afterward

Returning to what we can make of the six ideas of the last 50 years provides a stepping stone to your futures as lifelong students of animal behaviour. The rigor of sexual selection will remain a key element in discovery of the details of mating behaviour and fitness in the next 50 years, largely because Darwin's sexual selection ideas are rational, durable, and available for tests via strong inference experiments. But the notions of serious sex differences in mating behaviour due to anisogamy and/or to parental investment are likely to fade away entirely as study of sex differences continues to expose that there is nothing so like a female as a male and *vice versa*. The fourth idea embodied in the notions that individuals of ether sex are "adaptively flexible" able to modify behaviour as social and ecological circumstances change will supply the future with unexpected observations of how individuals modify their behaviour to enhance their fitness. The fifth idea about the way parents compensate for offspring viability deficits when they are forced or coerced to mate with partners they do not prefer is a serious issue (think: humans) associated most often in humans with males' attempts to control females' reproductive decisions. Understanding how compensatory effects change fitness trajectories of individuals is likely a high cost to parental lifespan. The sixth idea embodied in the Switch Point Theorem will organize a reimagining of how stochastic effects on an individual's lifespan, their encounters with potential mates and the durations of their time-outs after a mating determine lifetime fitness. Finally, there is more to come, as you imagine ideas beyond what you read and then discover what is not yet known!

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15

PARENTAL BEHAVIOUR

Juana Luis and Luis O. Romero-Morales

1.1 Introduction

Parental behaviour includes both maternal and paternal behaviours; in vertebrates this behaviour relates to a variety of parental repertoires from nest building, egg attending, brooding, food provisioning, nursing and carrying the young, defense of offspring, and socialization. Parental care has a significant effect on the survival and development of the offspring (Dulac et al. 2006). In mammals, females have the capability of raising the young alone. Females produce milk to feed their young and display various behaviours aimed at ensuring their survival. Mothers can perform several activities depending on the degree of development of the pups at birth. For example, when the pups are altricial (they are born naked, with their eyes and ear canals closed, and without the capacity to move and thermoregulate), the mothers of many species build a nest, crouch over, and retrieve the pups in addition to feeding and grooming them. However, when the pups are precocial (they are born fully developed and shortly after birth, they are capable of following their mothers), the mothers generally provide feeding and grooming (Lonstein et al. 2015). The mothers also protect their young from attacks by predators and from adult male conspecifics (Stolzenberg and Mayer 2019). This chapter addresses parental behaviour in mammals, particularly in rodents, which are the main models in the study of this area.

In mammals, from gestation until the pups are weaned, a close mother–pup relationship is established; in humans, this link persists throughout life. In primates and rodents, it has been shown that the separation of the mother from the pups for short periods affects long-term behavioural and cognitive aspects of their pups. Likewise, in biparental species, deprivation of paternal care causes severe alterations in the brain and behavioural development of the offspring (Dulac et al. 2014).

In mammals, the father's participation in the care of the pups is not common. However, in about 5% of mammalian genera, fathers provide care for their pups. Paternal behaviour is integrated by all the activities carried out by the father for the benefit of the young, which favor their survival (Clutton-Brock 1991). Paternal care activities have been observed in canids, rodents, and primates (Kleiman and Malcolm 1981).

Several species of biparental rodents, including the California mouse (*Peromyscus californicus*), the Mongolian gerbil (*Meriones unguiculatus*, dwarf hamster (*Phodopus campbelli*), mandarin vole (*Microtus mandarinus*), and prairie vole (*M. ochrogaster*) amomg othersbeen used as models for studying the neuroendocrine mechanisms that regulate paternal behaviour although some studies in primates, including human species, have been done (Lonstein et al. 2015; Horrel et al. 2018).

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1.2 Direct and indirect paternal care

Fathers, particularly in rodents, can provide direct and indirect care to their young. Direct paternal care has a direct benefit on the young. Among these parental actions are crouching over pups, grooming, pup retrieval, and socializing their offspring (Figure 15.1), while construction and maintenance of the nest in addition to vigilance and food provision (the father brings food back for the mother and pups) are considered indirect paternal care (Elwood 1983).

An understanding of the mechanisms that regulate parental behaviour includes an analysis of the hormonal, neural, and sensory factors that underlie this behaviour.

2.1 Hormonal regulation

In mammals, experimental evidence obtained mainly from studies with the laboratory rat (*Rattus norvegicus*) has shown that estradiol (E_2), progesterone (P_4), and prolactin (PRL), in addition to the neuropeptides, oxytocin (OT) and arginine-vasopressin (AVP), are involved in the regulation of maternal behaviour (Bridges 2015; Lonstein et al. 2015). Just as in females, males of biparental species must undergo hormonal changes to display paternal behaviour although they are not subject to the same hormonal changes as those that occur during pregnancy and parturition. Steroid hormones, such as testosterone (T) and its metabolites, E_2, dihydrotestosterone (DHT), and P_4 are involved in the regulation of this behaviour. Furthermore, as in maternal behaviour, PRL, AVP and OT have also been associated with the regulation of paternal behaviour (Lonstein et al. 2015; Horrel et al. 2018). However, causal roles in the activation of paternal behaviour have only been demonstrated for T and its metabolites (Trainor and Marler 2001, 2002; Martínez et al. 2015; Romero-Morales et al. 2018).

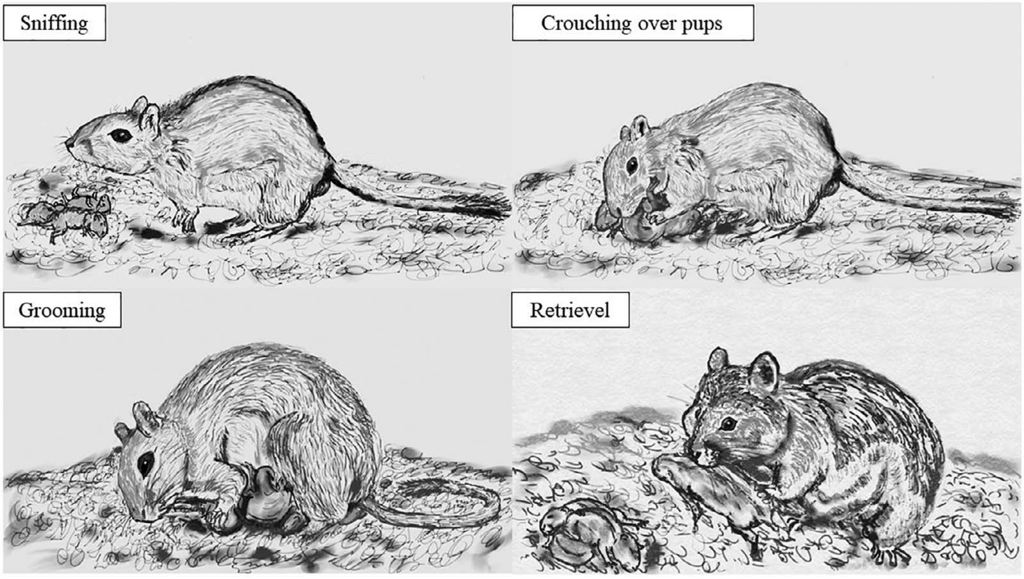

Figure 15.1 Direct paternal care in the Mongolian gerbil and dwarf hamster.

Drawings made by Eduardo Loya-Zurita.

2.2 Steroid hormones

The role of E_2 and P_4 in the regulation of maternal behaviour has been extensively analyzed, and numerous studies have shown that E_2 has an important role in initiation of maternal behaviour. In the rat during early pregnancy, P_4 concentrations increase, but the concentrations of this hormone decrease when the mother approaches parturition, while that of E_2 increases. This hormonal change, specifically the increase in E_2, has an essential role in the onset of maternal behaviour. Experiments with ovariectomized virgin female laboratory rats have shown that administration of a single injection of estradiol benzoate (100 μg/kg) shortened the latency of the onset of maternal behaviour (Siegel and Rosenblatt 1975). In other mammals, such as ungulates, carnivores, some primates, and sheep, this pattern of decreased P_4 and increased E_2 is similar to that observed in the rat although it differs with respect to the time at which the P_4/E_2 ratio changes (Lonstein et al. 2015). However, when E_2 is give in combination with P_4 mimicking hormonal changes that occur in late pregnancy, the effect of E_2 during the onset of maternal behaviour is more effective (Bridges 1984). Postpartum maternal behaviour is not affected by hypophysectomy and ovariectomy. This behaviour is dependent upon stimulation from pups; if the pups are removed after parturition, a decline in maternal behaviour could be observed after two to four days (Lonstein et al. 2015)

Regarding the role of T in the regulation of paternal behaviour, concentrations of this hormone appear to correlate with paternal behaviour. In a first study in male dwarf hamsters, it was observed that plasma T levels decreased when males provide paternal care (Reburn and Wynne-Edwards 1999). Subsequently, it was reported that in this rodent, T concentrations did not decrease when the rodents become fathers (Schum and Wynne-Edwards 2005). In the dwarf hamster, castration caused a significant reduction in T and E_2 levels, but paternal responsiveness was not affected (Hume and Wynne-Edwards 2005).

Subsequently, it was reported that in this rodent, T concentrations did not decrease when the rodents become fathers (Schum and Wynne-Edwards 2005). In the dwarf hamster, castration caused a significant reduction in T and E_2 levels, but paternal responsiveness was not affected (Hume and Wynne-Edwards 2005).

We showed that sexually inexperienced, castrated dwarf hamsters that were aggressive toward pups assumed paternal behaviour after receiving E_2 replacement. However, in males that are spontaneously paternal, these treatments do not cause any effect on paternal behaviour (Romero-Morales et al. 2018a). The differences among the results from Wynne-Edwards's research group and those obtained by our group appear to be due to the experimental designs. We used sexually inexperienced males; furthermore, before starting the treatments, the hamsters were exposed to pups of the species, so we knew whether these were aggressive or paternal toward the pups since males that were already fathers showed paternal behaviour.

In the California mouse, castration decreases the amount of parental care, whereas castrated males that receive T replacement display more paternal care (Trainor and Marler 2001). In this rodent, castrated males with sexual experience treated with T or E_2 displayed significantly higher huddling and grooming behaviour compared with males that received DHT or empty implants (Trainor and Marler 2002). Further, treatment with T plus aromatase inhibitor, an enzyme that converts T to E_2, blocks the positive effect of this androgen on paternal behaviour (Trainor and Marler 2002). In this rodent, the fathers have significantly more aromatase activity in the medial preoptic area (mPOA), which is a critical region involved in the regulation of parental behaviour, than mated males without pups, suggesting that an increase in E_2 production in this brain area promotes paternal behaviour (Trainor et al. 2003).

In the Mongolian gerbil, males with low concentrations of T were more paternal than males with normal circulating levels of T (Clark and Galef 1999). According to these results, T has a negative effect on paternal behaviour. However, we showed that sexually inexperienced gerbils that behaved aggressively toward pups of the same species exhibited paternal behaviour when they were treated with this androgen. In this rodent, T appears to exert its effects through its metabolites, E_2 and DHT, because gerbils demonstrating aggressive behaviour toward pups transition to paternal behaviours (exhibiting crouching over and grooming the pups) when E_2 or DHT concentrations increase as a consequence of replacement with these hormones after bilateral castration (Martínez et al. 2015). Thus, T seems to have an indirect role on regulation of paternal behaviour in the Mongolian gerbil, acting as a substrate for aromatase and reductase. This process could involve E2 and androgen receptors; in support of this proposal, we found that paternal gerbils compared to aggressive ones have significantly higher amounts of estrogen alpha and androgen receptors in the mPOA (Martínez et al. 2019).

In the cotton-top tamarin (*Saguinus oedipus*), it was shown that urinary T levels remained elevated when the males displayed paternal behaviour (Ziegler and Snowdon 2000). In contrast, in humans T levels decrease when they become fathers (Fleming et al. 2002), and human fathers with reduced basal T provide more paternal care than these with high levels of T (Kuo et al. 2016). Although most studies report that T facilitates the deployment of paternal care, more research is necessary to establish whether this hormone exerts its effects through its transformation to E_2 or through its two metabolites E_2 and DHT.

The limited data on the role of P_4 in regulating paternal behaviour indicate that this hormone has an inhibitory role in the regulation of paternal behaviour. In the California mouse, P_4 concentrations are lower in fathers compared to sexually inexperienced males (Trainor et al. 2003). However, in dwarf hamster males, P_4 levels increased after the birth of their pups when compared with *Phodopus sungorus*, a uniparental species (Schum and Wynne-Edwards 2005).

2.3 Prolactin

Prolactin (PRL) is a polypeptide hormone that is synthetized mainly in the anterior pituitary gland, although this hormone can also be produced in the nervous system, in the uterus, and even by the immune system. One of the well-known functions of PRL is its participation in the regulation of lactation; however, this hormone is also involved in multiple functions, for example, growth and the regulation of parental behaviour (Lonstein et al. 2015; Horrel et al. 2018).

PRL facilitates the onset of maternal behaviour as was demonstrated in virgin female hypophysectomized rats primed with P_4 and E_2 that displayed maternal behaviour more quickly than comparable females that were not treated with PRL (Bridges et al. 1985). Infusions of PRL into the mPOA of gonadectomized steroid-treated virgin rats that were treated with bromocriptine, a dopamine agonist that inhibits pituitary prolactin synthesis, stimulated the rapid onset of maternal behaviour toward foreign pups (Bridges and Ronsheim 1990). Females of the Cin85-deficient (Cin85−/−) laboratory mouse have a reduction in PRL secretion although their offspring develop normally; however, when their daughters become mothers, they present affectation in the expression of nurturing behaviours, for example, pup retrieval decreases (Sairenji et al. 2017). The results of these studies indicate that PRL promotes the onset of maternal behaviour, but its effects depend on previous stimulation with E_2 and P_4.

In addition to T in males, PRL is one of the hormones that has been most correlated with paternal behaviour. In biparental rodents, such as the California mouse, dwarf hamster, and the Mongolian gerbil, PRL concentrations were shown to be significantly increased in fathers that give care to their pups (Horrel et al. 2018). In several species of primates, males that interact with their pups have high concentrations of PRL, for example, in common marmosets (*Callithrix jacchus*) males that carry their pups show higher levels of PRL than males that do not carry their pups (Dixson and George 1982). Likewise, in the titi monkeys (*Callicebus cupreus*), fathers that carry infants also demonstrated higher PRL levels than non-fathers (Schradin et al. 2003). In humans, when fathers provide parental care, PRL concentrations increase, for example, fathers with higher concentrations of PRL were shown to be more responsive to their babies' cues than non-fathers (Fleming et al. 2002). Likewise, fathers who interact with their children demonstrated higher PRL levels than non-fathers (Gettler et al. 2012).

Although in a good number of biparental mammals, PRL concentrations increase when they become fathers, a manipulative study done with dwarf hamsters reported that experimentally suppressed PRL production in the pituitary failed to alter paternal behaviour. However, PRL produced in the brain could be involved in the regulation of paternal behaviour (Brooks et al. 2005).

2.4 Oxytocin

OT is a neuropeptide synthesized in the nerve cells of the paraventricular nucleus of the hypothalamus, after which it is transported by the axons of the hypothalamic neurons until it reaches the posterior portion of the neurohypophysis. OT participates in the partum regulation mechanisms and lactation (Yoshihara et al. 2018). OT has been implicated in a variety of pro-social behaviours, such as mating in monogamous species, and social memory. This neuropeptide also acts in the regulation of sexual, aggressive, and parental behaviour (Dumais and Veenema 2016). In the brain, neurons that produce OT project into critical regions that regulate maternal behaviour, such as the mPOA, the bed nucleus of stria terminalis (BNST), and amygdala (Kim et al. 2016).

In the rat, E_2 implants in the mPOA promote maternal behaviour through effects of E_2 on the OT receptor (Fahrbach and Pfaff 1986). In this rodent, infusions of OT antagonist into the ventral tegmental area or the mPOA inhibit the display of pup retrieval and the mothers'nursing postures (Pedersen et al. 1994).

The presence of OT or its receptor in neural areas that participate in the regulation of parental behaviour have been associated with the exhibition of paternal behaviour. In meadow voles (*Microtus pennsylvanicus*) with facultative paternal care (the male only provides care for his young in winter when he returns to cohabit with the female), the males with paternal experience had more receptors for OT in the BNST, lateral septum, and lateral amygdala than virgin males (Parker and Lee 2001). In the prairie vole, males with paternal experience had a higher number of oxytocin-immunoreactive neurons in the paraventricular nucleus of the hypothalamus than virgin males (Kenkel et al. 2014). In the California mouse, first-time fathers demonstrated significantly lower expression of the OT receptor mRNA in the BNST than virgin males. In other areas, such as the mPOA and medial amygdala (MeA), no significant differences were observed in the expression of the OT mRNA between fathers and virgin males (Perea-Rodríguez et al. 2015). In the mandarin vole, males mated with a female, that is, repeatedly exposed to pups of the species and fathers, as well as first-time male fathers provided more paternal care than sexually inexperienced males. Likewise, these males showed an increase in the expression of the OT mRNA and its receptors in the paraventricular nucleus and the supraoptic nucleus of the hypothalamus than sexually inexperienced males (Song et al. 2010). In the prairie vole, virgin males exposed to foreign pups of the species showed an increase in the peripheral concentration of OT (Kenkel et al. 2012). Li et al. (2015) showed that in the Mandarin vole, virgin males with a high paternal response (frequency of licking and grooming) had higher amounts of neurons immunoreactive to OT in the paraventricular nucleus and supraoptic nucleus of the hypothalamus compared to the males with low paternal responses. In this rodent, second-time fathers were shown to display more paternal care than first-time fathers, which suggests that the paternal experience significantly influences the levels of paternal behaviour, and that the amount of paternal care is associated with the presence of the OT receptor in the nucleus accumbens and medial amygdala (Wang et al. 2018). The results of these studies suggest that OT and its receptors are involved in the neuroendocrine mechanisms that regulate paternal behaviour.

2.5 Arginine-vasopressin

AVP is a neuropeptide that is synthesized in the hypothalamic supraoptic and paraventricular nuclei. This peptide is stored in and released by the posterior pituitary or neurohypophysis. AVP participates in the regulation of osmotic and cardiovascular homeostasis. In the brain, AVP is involved in

Table 15.1

Species	*Testosterone*	*Estradiol*	*Dihidrotestosterone*	*Progesterone*	*Prolactin*	*Vasopressin*	*Oxytocin*
California mouse *Peromyscus californicus*	Facilitates paternal behaviour (Trainor and Marler, 2001)	Facilitates paternal behaviour (Trainor and Marler, 2001; Trainor *et al.*, 2003)	Has no effect (Trainor *et al.*, 2002)	Decrease (Trainor *et al.*, 2003)	Increase (Gubernick and Nelson, 1989)	Nd	Decrease compared to expentat father and no change compared to virgin males (Gubernick *et al.*, 1995)
Mexican volcano mouse *Neotomodon alstoni*	Triggers the onset of the paternal behaviour (Luis *et al.*, 2012)	Nd	Nd	Nd	Nd	Nd	Nd
Dwarf hamster *Phodopus campbelli*	Has no effect (Hume and Wynne-Edwards, 2005; Schum and Wynne-Edwards, 2005)	Has no effect (Hume and Wynne-Edwards, 2005; Schum and Wynne-Edwards, 2005). Triggers the onset of the paternal behaviour (Romero-Morales *et al.,* 2018)	Nd	Nd	Increase in paternal males (Reburn and Wynne-Edwards, 1999)	Increase (Reburn and Wynne-Edwards, 1999).	Nd
Mongolian gerbils *Meriones unguiculatus*	Decrease paternal behaviour (Clark and Galef, 1999). Triggers paternal behaviour (Martínez *et al.*, 2015)	Triggers paternal behaviour (Martínez *et al.*, 2015)	Triggers paternal behaviour (Martínez *et al.*, 2015)	Nd	Increase (Brown *et al.*, 1995)		Nd

the modulation of various social behaviours, such as pair-bonding, pair recognition, and parental and aggressive behaviours (Horrel et al. 2018). In the rat, near parturition causes release of AVP and OT in addition to increased AVP receptor expression in the mPOA (Lonstein et al. 2015).

In prairie voles, AVP injections into the lateral septum caused an increase in crouching over pups and grooming by sexually inexperienced males, while administration of an antagonist of receptor V1a of vasopressin inhibited paternal behaviour in a dose-specific manner, suggesting that septal AVP increases paternal responsiveness via a receptor-mediated mechanism (Wang et al. 1994). In this rodent, castration was shown to reduce vasopressinergic projections in BNST and MeA, indicating that AVP projections are testosterone-dependent (Wang and De Vries 1993).

3.1 Neural regulation

Since Numan (1988) proposed the first maternal behaviour regulatory circuit based on the results of studies carried out with the laboratory rat, several models of the maternal behaviour neural circuit have been constructed. Construction of this circuit depended upon the results of studies of lesions, stimulation, neural activation markers, such as as c-fos, Fos β, and glucose uptake (Horrel et al. 2018).

Numan (1988) proposed the neural and motivational models of the control of maternal responsiveness from the perspective of avoidance; this model suggests maternal behaviour is displayed when the tendency to approach and interact with stimuli from the pups is greater than the tendency to avoid those stimuli. The mPOA and the BNST are considered primary excitatory nuclei because they send information to the mesolimbic dopamine system for display of maternal behaviour, whereas the anterior hypothalamic (AHN), ventromedial hypothalamic (VMH), and periaqueductal gray nuclei (PAG) are considered inhibitory toward maternal behaviour (Figure 15.2). Currently, the neural circuit model of maternal behaviour is very complex. Stimuli from the pups are transmitted from the olfactory bulb (OB) to the MeA that, in turn, communicates with the BNST after this information is processed in mPOA and BNST. The amygdala also directly sends sensory information to the AHN and the VMH. The maternal or avoidance response depends on the physiological condition of the female, especially her hormonal status (Horrel et al. 2018). Vast experimental evidence has shown that the mPOA has a central role in the expression of maternal behaviour; in this brain area, integrated

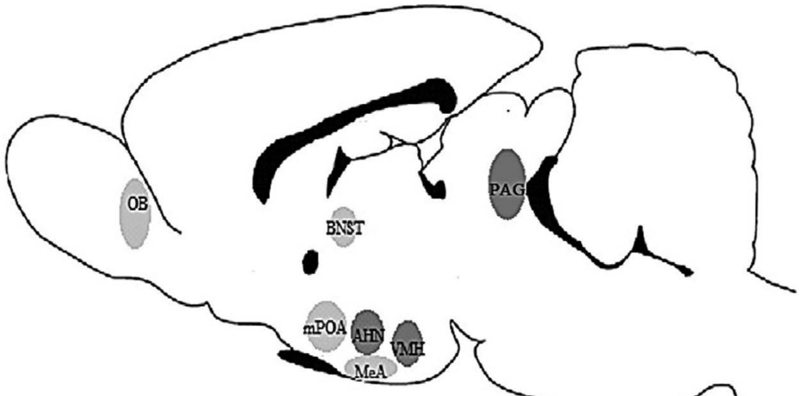

Figure 15.2 Schematic representation of a sagittal section of rat brain showing the location of the different neural regions that regulate parental behaviour, such as medial preoptic area (mPOA), bed nucleus of the stria terminalis (BNST), anterior hypothalamic nucleus (AHN), ventromedial hypothalamic (VMH), periaqueductal gray (PAG), medial amygdala (MeA) and olfactory bulb (OB).

sensory input pathways under influence of hormonal milieu exist (Horrel et al. 2018). It has been suggested that the mPOA facilitates maternal behaviour by inhibiting the nuclei involved in the avoidance behaviour and by exciting the reward circuitry via projections to the ventral tegmental area in the midbrain and nucleus accumbens in the forebrain. In the mPOA at the end of pregnancy, a significant presence of E_2, PRL, OT, and AVP receptors can be found, indicating that this region is one of the main areas of the brain in which hormones involved in the regulation of maternal behaviour exert their effects (Lonstein et al. 2015; Horrel et al. 2018).

In mammals, it has been suggested that brain networks regulating maternal and paternal behaviour are homologous. It then might be expected that the same areas that regulate maternal behaviour are also involved in regulating paternal behaviour, and this homology also includes neuroendocrine circuits (Lonstein et al. 2015). Studies conducted to date on the neural regulation of paternal behaviour support this assumption. In the California mouse, electrolyte lesions in the mPOA, nucleus accumbens, and MeA cause a decrease in the time invested by fathers in retrieving, crouching, and grooming pups. Furthermore, only 12.5% of the lesioned males displayed paternal behaviours (Lee and Brown 2002, 2007). In prairie voles, interactions among male-pup activating regions such as the mPOA, BNST, lateral septum, and MeA were assessed by using *c-fos* as a marker of neuronal activity (Kirkpatrick et al. 1994). In the Mongolian gerbil, sexually inexperienced males that paternally interacted with foreign pups of the same species were shown to have a significantly higher number of c-fos immunoreactive cells in the mPOA and BNST than those that interacted with candy. When males that were aggressive toward pups interacted with the pups, AHN, VMH, and PAG nuclei were significantly activated. The MeA and OB presented the same level of activation in paternal gerbils and those that were aggressive with the pups as shown in Figure 15.3 (Romero-Morales et al. 2018b). The few studies on the neural regulation of paternal behaviour indicate that at least at the anatomical level there is homology in the neural regulation of maternal and paternal behaviour.

4.1 Detection and processing of signals from the pups

For the display of parental care to take place, the parents must be able to accurately recognize their pups to establish the physical proximity required for the execution of this care. The mechanisms through which recognition occurs vary according to species; these can involve sensory stimuli, such as vision, hearing, taste, touch, and smell (Lonstein et al. 2015).

Olfactory stimuli in mammals, specifically in rodents, have great relevance in the display of social behaviours such as parental behaviour (Sanchez-Andrade and Kendrick 2009). In female laboratory rats, bulbectomy (removal of the olfactory bulbs) or treatment with zinc sulfate, a substance that causes anosmia (loss of smell), which destroys the olfactory epithelium, significantly reduces maternal care. In rodents, smell is the main sensory input for stimuli from pups (Fleming and Rosenblatt 1974). Following bilateral olfactory bulbectomy in male prairie voles, decreases in measures of sexual, paternal, and other social behaviours were observed, but were not evident with unilateral or sham bulbectomy (Kirkpatrick et al. 1994). Apparently, the olfactory stimuli from the pups are processed in the same neural regions in males and females, due to the fact that both sexes present parental or aversive behaviours (Dulac et al. 2014; Romero-Morales et al. 2018b). This duality in the parental response corresponds at the neural level with regions involved in promoting the parental response and others involved in inhibiting this behaviour (Numan and Insel 2003). It should be noted that these neural circuits are just a small part of the mechanisms involved in the regulation of parental behaviour; this is because the neural circuits that mediate signals from sensory stimuli, such as vision, hearing, and smell, are still unknown (Horrel et al. 2018).

In rats, vision and hearing do not affect maternal behaviour, as demonstrated by a study showing that rats whose eyes are removed or sutured closed before parturition did not show differences in maternal care compared with rats whose eyes were not removed or sutured (Kolunie et al. 1994). Regarding hearing, it has been observed that rats and mice that are mothers can detect their pups'

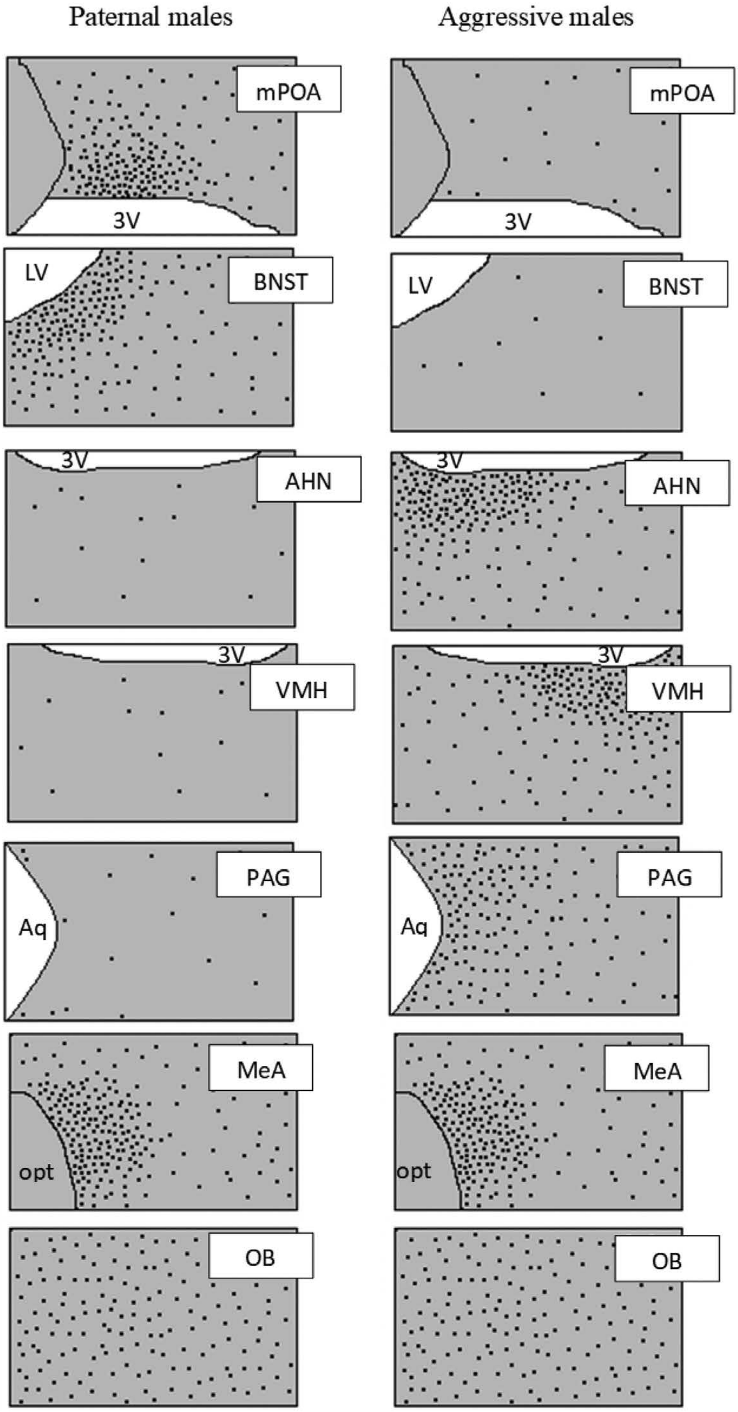

Figure 15.3 Schematic representation of coronal sections of paternal and aggressive males in the medial preoptic area (mPOA), bed nucleus of the stria terminalis (BNST), anterior hypothalamic nucleus (AHN), ventromedial hypothalamic (VMH), periaqueductal gray (PAG), medial amygdala (MeA) and olfactory bulb (OB) showing the location of c-Fos-immunoreactive cells after interaction with pups. 3V = third ventricle, LV = lateral ventricle, Aq = aqueduct, opt: optic tract.

Source: Modified from Romero-Morales et al. 2018b.

vocalizations and even discriminate their sex (Bowers et al. 2013). However, the vocalizations of their pups do not seem to influence maternal behaviour (Farrell and Alberts 2002). There are, to date, no studies that indicate that the vocalizations emitted by the pups and the visual stimuli stimulate paternal behaviour.

It has not been examined in detail whether taste influences the maternal and/or paternal behaviour of any species, but when anesthesia is applied to the tongue of a laboratory rat, licking is significantly reduced, but not retrieval of pups (Stern and Johnson 1989). These results are difficult to interpret because anesthesia to the tongue affects both taste and somatosensory inputs (all those sensations related to touch and temperature) (Jacquin and Zeigler 1984).

After mother rodents have been attracted to their pups through distal signals (hearing, vision, and smell) and then through the perioral and ventral somatosensory stimulation that they receive from the pups, which are an essential stimulus, they perform maternal behaviour (Stern 1996). Grooming and retrieval of pups are inhibited when the perioral area is anesthetized, or surgery is performed to cut the nerves that transmit somatosensory stimuli (Stern 1996). Likewise, lactation, in the case of females, is facilitated by the stimuli of the pups sucking the mammary glands. These stimuli allow the maintenance of lactation behaviour (Magnusson and Fleming 1995). For example, when the pups are anesthetized in the perioral region and cannot carry out the suction of the nipple, the female, not receiving these stimuli, moves away from the nest and does not continue to suckle the pups (Stern and Johnson 1989). These types of studies have not been carried out in males since lactation is an exclusive component of maternal behaviour.

4.2 Experience and parental behaviour

Several studies have shown that maternal experience influences maternal behaviour; females of laboratory rats that after parturition had minimal social experience with their pups display significantly longer onset latencies of maternal behaviour than those that interact with their pups 2 or 24 hours. Further, females with maternal experience are capable to retain the maternal response for up to 30 days after delivery (Orpen and Fleming 1987; Fleming and Sarker 1989). There is strong evidence that both maternal and paternal behaviour are affected by experiences during the first days of life; for example, female pups that receive large amounts of grooming when they are mothers also provide their pups with a lot of grooming (Champagne et al. 2001). In several species of biparental rodents, it has been shown that the lack of parental care causes serious disorders in the paternal behaviour of individuals when they are adults, for example, in the mandarin vole, the lack of parental care decreases the retrieval pups (Yu et al. 2015).

5. Conclusions

Vast experimental evidence supports that the onset of maternal behaviour is triggered by the change in the concentration of P_4 and E_2 at the end of pregnancy. However, there are still few studies that postulate that the onset of paternal behaviour is dependent on T. In addition, there is the possibility that in some species of rodents T may exert its effects through its conversion to E_2 and in others through the androgenic and estrogenic pathway. Regarding neural regulation, everything seems to point out that the neural regions that regulate maternal behaviour also participate in the regulation of paternal behaviour, although lesson studies are required to establish conclusively the function of these neural areas in the regulation of this behaviour. Currently, studies of neural regulation of behaviour with the use of optogenetic techniques are identifying subnuclei of neurons involved in the regulation of parental behaviour. In rodents, it has been widely shown that smell is one of the main sensory factors that regulate maternal behaviour, but it is unknown whether the same could apply to parental behaviour. Due to the essential role of maternal behaviour in the survival of mammals, the neuroendocrine and sensory mechanisms that regulate this behaviour can be framed in a general pattern.

However, paternal behaviour is present in several species of rodents that are not phylogenetically close so that it might be expected that the mechanisms for regulating this behaviour might not conform to a general pattern.

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16

PLAY BEHAVIOUR

A COMPARATIVE PERSPECTIVE

Elisabetta Palagi and Sergio Pellis

Introduction

The last two decades have seen an increasing number of studies focusing on play and its possible functions in human and non-human animals (Pellegrini 2011; Smith and Roopnarine 2019). The increasing interest has unveiled many important new insights about this enigmatic behaviour, although the lack of agreement on how to study play has also led to confusing and contradictory findings. Operationally defining play is far from easy. The most comprehensive definition available lists five criteria that a behaviour should fulfil to be categorized as play (Burghardt 2005). While applying this 5-criteria definition has been very helpful in ensuring that researchers studying different species are converging on comparable behaviour, there are some limitations in this approach that have caused continuing difficulties in identifying play. Using empirical examples, we reveal which of these criteria can be readily applied, which are difficult to apply and which need modification.

> *The first criterion for recognizing play is that the performance of the behavior is not fully functional in the form or context in which it is expressed; that is, it includes elements, or is directed toward stimuli, that do not contribute to current survival.*
>
> *(Burghardt 2005)*

This criterion is the most difficult to demonstrate empirically, because many different behaviours do not have a fully functional goal. For example, misdirected behaviours (e.g., dogs mounting their owner's leg), self-directed behaviours (e.g., self-scratching), and vacuum behaviours (e.g., insectivorous birds engaging in actions such as catching and consuming an imaginary prey) are non-playful activities that do not contribute to current survival. Also, there are examples that illustrate how the mixing of functional and non-functional sequences can occur in a playful context. For example, hamadryas baboons (*Papio hamadryas*) can engage in "stone handling", a solitary playful activity during which the animal manipulates stones (Nahallage et al. 2016). In some cases, this playful activity can be intermixed with tool-use activities during which the stone is used to reach specific goals. For example, when an animal juggles the stone in the air the behaviour is clearly *not fully functional in the form in which it is expressed*, but when the subject rubs that stone on its genitalia, there is a functional element, as the monkey can gain sexual gratification (Cenni et al. 2020).

Focusing on the absence of the current function of the behaviour, much of the play seen among adults can be excluded, as in many cases the behaviour can serve immediate functions (Nahallage et al. 2016; Palagi 2011). For instance, play fighting, a commonly reported form of social play (Aldis 1975;

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Fagen 1981), can function in adulthood as a non-agonistic form of interaction to test and reinforce social relationships (Pellis 2002). In this case, whether play fighting involves immature or adult animals, to be consistent with criterion #1 it needs to be demonstrated that play fighting does not serve the functions associated with those same actions performed during serious fighting. That is, to apply this criterion rigorously, playful actions and their contexts of use need to be thoroughly analyzed.

> *The second criterion for recognizing play is that the behavior is spontaneous, voluntary, intentional, pleasurable, rewarding, reinforcing, or autotelic ("done for its own sake").*
>
> *(Burghardt 2005)*

Animals engage in playful activities in a spontaneous way and not in response to apparent external stimuli, thus suggesting that endogenous factors may be at the basis of the urge to play. Some acrobatic/locomotor maneuvers that monkeys and apes suddenly engage in illustrate this concept (Palagi 2018; Pellis and Pellis 2009). The subject's action is not in response to a given stimulus (*spontaneous*) except when he/she is actively invited to play by conspecifics (*intentional*) or tends to imitate their partner (*reinforcing*). Thus, it could be concluded that play stimulates play (*done for its own sake*). For example, Reinhold and coworkers (2019) played hide-and-seek with adolescent male rats that not only learned the game but also learned to shift their roles as hiders or seekers. During the training, the rats were rewarded by being tickled by an experimenter. The rats adjusted their behaviour as a function of their role in the game. As seekers, rats emitted vocalizations, but when hiding, they vocalized less and preferred opaque over transparent hiding shelters. The rats executed "joy jumps" and quick, frantic searching and teasing of the experimenter. Once found, the rats often ran away and re-hid: thus suggesting that what was most rewarding was not being tickled, but the continuation of the game. As a whole, these findings support the *Play-to-Play Hypothesis* predicting that play is *self-reinforcing* and so an *autotelic* activity.

> *The third criterion for recognizing play is that it differs from the "serious" performance of ethotypic behavior structurally or temporally in at least one respect: it is incomplete (generally through inhibited or dropped final elements), exaggerated, awkward, or precocious; or it involves behavior patterns with modified form, sequencing, or targeting. The fourth criterion for recognizing play is that the behavior is performed repeatedly in a similar, but not rigidly stereotyped, form during at least a portion of the animal's ontogeny.*
>
> *(Burghardt 2005)*

These criteria appear clear when looking at the ontogenetic pathways of our phylogenetically closest relatives: chimpanzees (*Pan troglodytes*) and bonobos (*P. paniscus*). In early infancy, both species show short playful social sessions that are often composed of the same motor patterns repeated several times. These play sessions are neither complex nor variable. This *precocious* (and monotonous!) form of play tends to become enriched with increasing age as the social network of the subject expands (Palagi and Cordoni 2012). During juvenile development, chimpanzees and bonobos engage in playful interactions that can include all elements of the behavioural repertoire they will show as adults. For example, during social play, young bonobos can incorporate behaviour patterns that are *ethotypically* performed during real agonistic encounters, socio-sexual behaviour (homo- and heterosexual patterns), affiliative interactions and mothering activity (Palagi 2018). Obviously, the patterns borrowed from the different domains are modified both *structurally* and *temporally,* so it is possible that while one of the players tries to bite the partner, the latter engages in a sexual interaction with a third playmate (*modified targeting*). Such modifications are not limited to juveniles.

Both immature and adult long-tailed macaques engage in play with stones, with most of the actions resembling those used during foraging (Pelletier et al. 2017). Adults can grasp a hard-shelled nut, raise it upwards and then smack it to the ground; eventually after repeated pounds, the shell cracks allowing the flesh of the nut to be removed and eaten. While immature monkeys do not crack nuts using this action, both adult and immature monkeys use the same pounding action when playing with stones. Both adult and immature modify the kinematics of the pounding of stones and this differs to the pounds adults deliver with nuts (Pellis et al. 2019a). That is, because both adults and juveniles converge on the same kinematics of pounding when playing with stones, the play pattern of the juveniles cannot be discounted as arising from sensorimotor immaturity. Rather, the modification arises because the action is performed in a playful context.

> *The fifth criterion for recognizing play is that the behavior is initiated when an animal is adequately fed, healthy, and free from stress (e.g., predator threat, harsh microclimate, social instability), or intense competing systems (e.g., feeding, mating, predator avoidance). In other words, the animal is in a "relaxed field".*
>
> *(Burghardt 2005)*

The hierarchical organization of behaviour is at the basis of this criterion. Play is an expendable behaviour if compared to other activities entailing immediate survival and increased reproductive opportunities. Hence, at first glance, play should have been selected against. However, data are emerging that play can provide future benefits even though there are immediate costs. For example, in *Macaca assamensis*, young males engage in more locomotor play than female peers, which corresponds with them acquiring motor skills faster than females, but given that to play more they spend less time eating males grow more slowly than females (Berghänel et al. 2015).

It is also important to note that it is severe stress that inhibits play, as low to moderate levels of stress can actually stimulate more play. Indeed, there are now examples in a variety of species showing that play can function to dampen stress in both immature and adult animals (Pellis and Burghardt 2017). For example, in a study on adult riding school horses (*Equus caballus*), Hausberger and coworkers (2012) recorded behavioural activity (including social play) and some indicators of stress (e.g., plasmatic cortisol concentrations, oxidative stress) and welfare (e.g., levels of aggressiveness against humans) when the animals were in their home stalls and when they were allowed to spend time in a paddock. In the paddock, horses scored much higher levels of play compared to those recorded in populations maintained in more natural conditions. Of greatest relevance to criterion #5, the most playful horses exhibited the most stress. It is possible that by playing, recovery from psychological/physical stress is facilitated and the animals increase their emotional resilience to unfavorable conditions. The modification to criterion #5 by such examples suggests that the presence of play cannot be automatically assumed to reflect low levels of stress, as has previously been thought to be the case in using play as a marker for animal welfare (Blois-Huelin et al. 2015; Held and Špinka 2011).

The 5-criteria definition and the phylogeny of play

Although the 5-criteria definition is not without problems, it has provided two major advances in identifying and characterizing play. First, by requiring that a behaviour meets all five criteria before qualifying as play, this definition has been able to differentiate play from other activities with which it shares some, but not all properties, such as exploration and stereotypies (Pellis and Burghardt 2017). Second, it has provided an objective framework with which to compare play-like behaviour across a diverse range of species. In doing so, play has been identified in vertebrates beyond mammals and birds and even some invertebrates (Burghardt 2005). Consequently, play requires deeper explanations that can apply across lineages with very different body morphologies and physiology, and neural and cognitive capabilities.

Nonetheless, of the 35 recognized animal phyla, only members of three phyla have been reported to play (Burghardt 2005; Burghardt and Pellis 2019). A few species of arthropods, such as insects and spiders (e.g., Dapporto et al. 2006; Pruitt et al. 2012), and for molluscs, a couple of species of octopus (Kuba et al. 2006; Mather and Anderson 1999), represent the sum total of the two phyla of invertebrates that have been reported to play. The majority of examples of play are in the vertebrates, but even in this group, play is only sporadic in fish, amphibians and reptiles (e.g., Burghardt, 2005; Burghardt et al. 2014; Dinets 2015). In part, this could be because of a sparseness of data, with few detailed studies having been conducted outside of mammals and birds. Although even in mammals and birds, lineages that provide the most extensive examples of play (Fagen 1981), not all lineages (and species within lineages of these taxa) engage in play (Burghardt 2005; Kaplan 2020). This suggests that while play may be widespread, it is sporadic in its phylogenetic distribution (Burghardt and Pellis 2019).

Another lesson drawn from these phylogenetic considerations concerns the type of play present. Typically, for non-human animals three types of play are recognized (Fagen 1981). These are locomotor play, involving an individual animal engaging in running, jumping, kicking and making turns (Figure 16.1A); object play, involving an individual animal engaging in carrying, flinging, ripping or otherwise manipulating an inanimate object; and social play, involving two or more conspecifics wrestling, chasing or otherwise manipulating one another (Figure 16.1B). Different taxonomic lineages tend to predominantly engage in different kinds of play, with some engaging in only one type, some two and a minority engaging in all three (Burghardt 2005). Even in those that have more than one type of play, one type may be predominant. For example, New World deer (*Odocoileus hemionus*, *O. virginanus*) engage in both locomotor and social play, but even when the opportunity is available, they are more likely to engage in locomotor play (Carter et al. 2019). Indeed, different types of play may be antithetical. For example, in rodents there is a negative correlation between locomotor and social play, with species that engage in more locomotor play engaging in less social play (Pellis and Iwaniuk 2004). In a few species from a limited number of lineages in which more than one type of play is present, elements from the different types of play can be mixed together (Burghardt et al. 2016; Shimada 2012). The evolution of types of play and their interrelationship remains unresolved (Pellis et al. 2019a).

Another problem with the designation of the three types of play is that it focuses on the target of the behaviour (one's own body, an inanimate object, a social partner), not on the actual behavioural patterns performed (Pellis and Pellis 2017a). For example, the locomotor play of many ungulates involves the playful execution of the runs, jumps, turns and other protean movements that are otherwise seen, functionally, in anti-predator behaviour (Byers 1984); in rats (*Rattus norvegicus*) the darts,

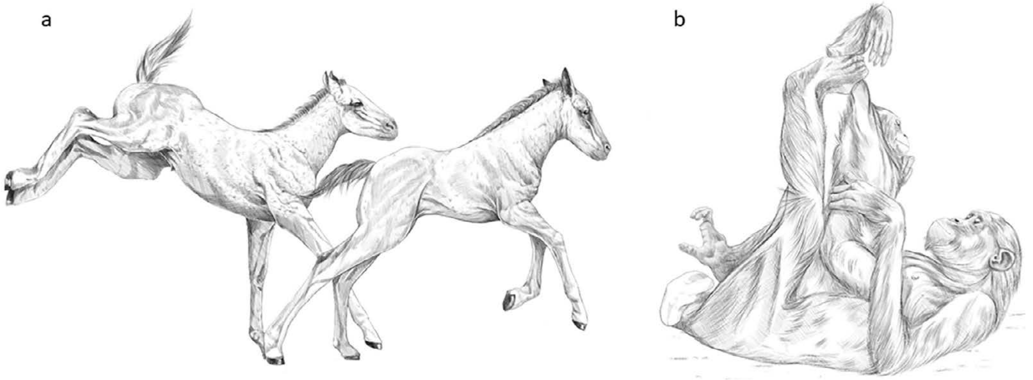

Figure 16.1 Examples of different types of play (A) locomotor-rotational play in foals, and (B) social play, involving maternal play, in bonobos.

(Drawings by Fosca Mastrandrea)

hops and runs performed during play are typical of sexually receptive adult females (Thor and Holloway 1984), whereas, in other species some of the locomotor behaviour may not be derived from other functional contexts and is thus unique to play, such as the pirouettes performed by chimpanzees (*Pan troglodytes*) (Nishida and Inaba 2009). Labeling all three as locomotor play may confound behavioural processes that are very different. For example, juvenile chimpanzees play with sticks, but there is a sex difference. Males wield and throw sticks, mimicking the aggressive displays of adult males, whereas females carry and cuddle sticks, mimicking the maternal behaviour of adult females (Kahlenberg and Wrangham, 2010). Conversely, cats may playfully direct predatory behaviour patterns to either inanimate objects, to prey or to conspecifics (Leyhausen 1979). The same kind of diversity is present in social play, which can involve behaviour patterns typical of nurturing young (play mothering), courtship and copulation (sex play) or conspecific aggression (play fighting) (Burghardt 2005; Fagen 1981; Pellis and Pellis 2009). Indeed, even 'play fighting' may be an amalgam of behavioural sequences that can involve competitive interactions of diverse origins: the animals may compete for contact with body targets typical of aggression, courtship, greeting or grooming (Pellis and Pellis 2017b, 2018). Although it has become commonplace to label play based on the target to which the behaviour is directed, it is not self-evident that this classification is superior to one based on the type of behaviour performed (Pellis and Pellis 2017a).

More detailed studies of diverse patterns of play across a wide range of species are needed to resolve the problem of how best to classify play, which is essential for making phylogenetic comparisons (Burghardt and Pellis 2019). In this regard, play fighting is a useful vehicle for drawing broad generalizations about play. There are several reasons for this. First, play fighting has been one of the forms of non-human play that has been most intensively studied (Pellis and Pellis 2009). Second, it occurs in a wide range of mammals and birds, allowing the comparison of similar behaviour across different species (Palagi 2018; Pellis and Iwaniuk 2004). Third, in its most complex form, play fighting engages some of the most sophisticated socio-cognitive skills available to a species. This latter point allows us to use this type of play as a window into the mind of animals (Palagi et al. 2016; Pellis and Pellis 2016).

Play fighting: a window into animal minds

Play fighting, a type of social play that is widespread in mammals, is one of the most iconic examples of how animals have to learn to cope with unpredictable situations (Palagi et al. 2016). As noted above, during play fighting animals compete to gain some advantage over their partner, but do so in a manner that can curtail their ability to gain or maintain that advantage (Figure 16.2). By doing so, the animals experience unpredictability and role reversals between play mates (Pellis and Pellis 2016, 2017b). This activity requires fine-tuned modulation due to the risk of misinterpretation of the "fighting" exchanges. Contrary to competitive structured games (e.g., football), during which the rules are universally established and often enforced by an umpire, free play necessitates that the players themselves accurately moderate the interaction by following some rules that are negotiated during the ongoing interaction. To do that, the patterns have to be performed in a highly controlled way via restraining strength, velocity and roughness of the motor actions and by signaling to the playmate that what is happening is not "serious". Comparative studies of primates have shown that relative brain size, and especially those areas involved in regulating play, correlates with the amount of social play (but not solitary play) in which they engage (Graham 2011). Similarly, among birds, relative brain size is larger in those species that play compared to those that do not, and it is significantly larger in those that engage in social play compared to those that engage only in object play (Kaplan 2020). Playing socially can, therefore, be a cognitively demanding activity that needs to be regulated by sophisticated communicative mechanisms based on clear signals that have a low likelihood of being misinterpreted (Bekoff 1995; Palagi 2007, 2008; Palagi et al. 2015).

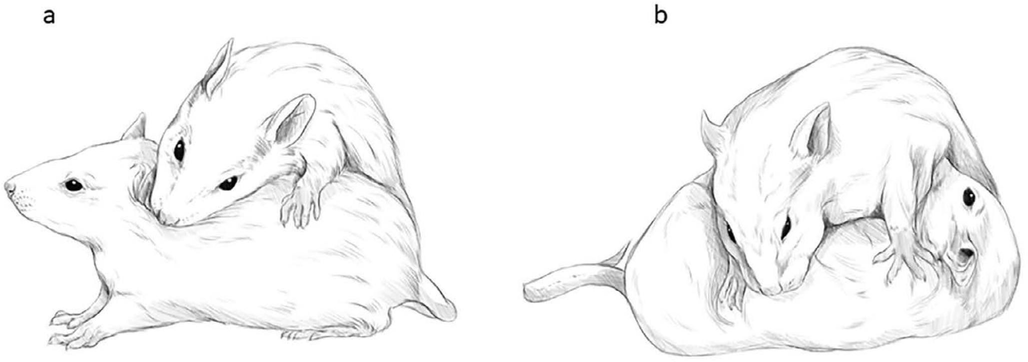

Figure 16.2 Two phases in the play fighting of young rats: (a) Attack of the nape of the neck, and (b) wrestling, as the recipient rotates onto its back to protect its nape.

(Drawings by Fosca Mastrandrea)

Play fighting and the development of the social brain

Studies with rodents have shown that play fighting with peers during the juvenile period provides experience that facilitates the development of socio-cognitive skills, and does so by modifying the anatomy and function of the prefrontal cortex – the region of the brain housing some of the neural circuits critical to these skills (e.g., Baarendse et al. 2013; Bell et al. 2010; Burleson et al. 2016; Marks et al. 2017; Schneider et al. 2016; Stark and Pellis 2020). As already noted, maintaining the balance between competition and cooperation that allows for play fighting to remain playful, requires at least occasional role reversals, and these are cognitively demanding (Pellis and Pellis, 2016, 2017b). Evidence suggests that it is the decision making needed for such reciprocation, rather than just performing playful actions, that is essential for training these socio-cognitive skills (Pellis et al. 2019b; Schneider et al. 2016). Also, it is the ability to modify the degree of reciprocity that appears to be important in using play fighting as a social tool to test and reinforce social relationships during adulthood (Pellis, 2002; Pellis et al. 1993; Smith et al.1999).

Communication between play partners is important for negotiating these reciprocal exchanges (Kisko et al. 2015). However, among rats the primary communication modality is auditory, using a variety of ultrasonic calls in association with performing particular actions, which can influence the actions performed by their partners (Burke et al. 2018, 2020). There are indications that calling back and forth between partners is critical in some situations to avoid misinterpretation and either cessation of play or its escalation to aggression (Burke et al. 2017). However, to be able to triangulate which partner is calling and identifying whether each is emitting a particular type of call is technically challenging (Sangiamo et al. 2020), especially during close quarter wrestling. Species that rely on visual signaling during play fighting have been a better model to explore these inter-individual communication exchanges.

Communicating play and its positive rewarding nature

Complex social interactions rely on complex forms of communication, and signals provide the key for allowing individuals to make adaptive behavioural decisions (Freeberg et al. 2012). To underline the playful nature of an interaction, animals make use of a large variety of signals, including facial expressions, postures, gestures and vocalizations, which are often intermixed to negotiate the encounter (Palagi et al. 2016). To invite conspecifics to play, ring-tailed lemurs (*Lemur catta*) anoint their tails with scent glands on their wrists and keep their ears upright while watching their potential play partners (Palagi 2009), dogs (*Canis lupus familiaris*) wave their tails while bowing and sometimes bark (Palagi et al. 2015) and some species of monkeys, such as the Hanuman langur (*Semnopithecus entellus*), rotate their heads while keeping them close to the ground (Petrů et al. 2008). All these postures are often accompanied by specific facial expressions.

A facial expression can convey information to a playmate about the motivational/intentional state of the sender who is aware that the message has arrived only if the receiver congruently replies to the stimulus perceived. For this reason, in the last decade several studies on playful facial communication have been devoted to understanding the presence and the possible roles of mimicry in modulating play sessions in both primates and other mammals (Palagi and Scopa 2017). The relaxed open mouth (ROM), also called the play face, is the typical facial expression punctuating the playful sessions of several species, including humans (van Hooff 1972). ROM occurs during play fighting in dogs (Palagi et al. 2015), meerkats (*Suricata suricatta*, Palagi et al. 2019), South American sea lions (*Otaria flavescens*, Llamazares-Martín et al. 2017), horses (*Equus caballus*, Maglieri et al. 2020), sun bears (*Helarctos malayanus*, Taylor et al. 2019), a number of primate species including prosimians (Palagi et al. 2014), monkeys (Mancini and Palagi 2013; Palagi and Scopa 2017) and great apes (Palagi 2006, 2007), and possibly in some birds, such as the Australian magpie (*Gymnorhina tibicen*) (Pellis, 1981).

Because of its rewarding nature, during play, animals experience a positive mood that is often expressed through ROMs. A ROM can elicit a rapid mimicry response in the observer in several primate and non-primate species. The unconscious and rapid replication of ROMs allows animals to share their playful mood that, in turn, seems to be particularly effective in building and reinforcing affective bonds. As a whole, rapid facial mimicry is informative about reciprocal attentiveness, social sensitivity and strong bonding (Palagi et al. 2019). Moreover, through reflexive mimicry, which involves mirroring the partner's facial expression, players inform each other that the signal has been correctly perceived and interpreted, thus making the interactions more successful. Supporting this interpretation is the finding that in many species mimicking others' ROMs rather than simply perceiving them, or responding with an incongruent expression, significantly prolongs the playful interaction (Figure 16.3). The challenge is to develop a multi-modal approach to the study of rapid mimicry. This would clarify if and how the integration of signals based on different sensory modalities (e.g., visual, acoustic, chemical) modulates motor resonance phenomena and consequently playful mood.

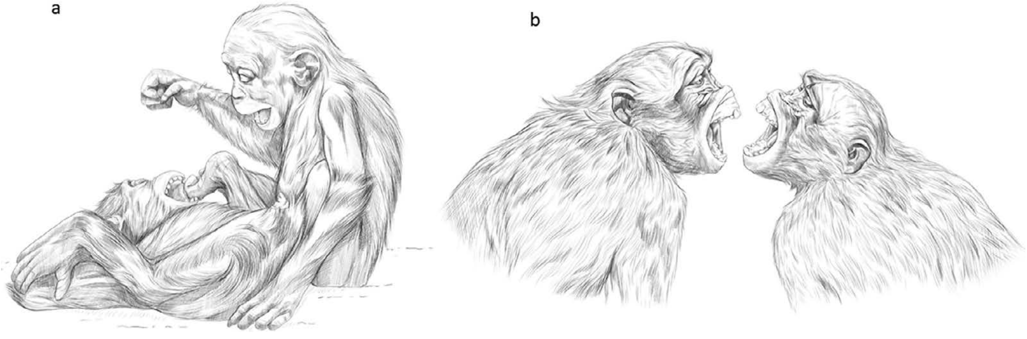

Figure 16.3 Communicating play: (a) Incongruent signaling in a pair of juvenile bonobos (upper teeth exposed in the seated partner, upper teeth exposed in the subject laying on its back), and (b) congruent signaling in a pair of sub-adult geladas (both have their upper teeth exposed).

(Drawings by Fosca Mastrandrea)

Conclusion

The advances in the study of animal play fighting have revealed three important lessons that may apply more broadly across other types of play. First, gradations in complexity of play fighting across species suggest that different lineages have undergone differing degrees of evolutionary change in this behaviour. Such change in play would be associated with modifications in the regulatory mechanisms involved (Burghardt and Pellis 2019). Second, whether the advantage competed over in play fighting is derived from aggressive behaviour, as in many primates and some rodents (Aldis 1975; Pellis and Pellis 2009; Symons 1978) or socio-sexual behaviour, as in many rodents and some primates (Pellis and Pellis 2009, 2018), when play evolves to a high degree of complexity, there is functional convergence. Play fighting during adolescence in some primates and rodents can facilitate the refinement of socio-cognitive skills (Palagi 2018; Pellis and Pellis 2017b). Third, the brain circuits needed to produce and regulate social play in rats have been well mapped out (Siviy 2016) and these match the relative size of brain regions associated with increased performance of social play in primates (Graham 2011), suggesting a common pan-mammalian neural system (Panksepp 1998).

Evolutionary changes in complexity of other types of play may follow similar patterns of transformation (Pellis et al. 2019a). For example, many of the behaviour patterns used in the stone play of macaque species are derived from the behaviour patterns used in foraging (Pelletier et al. 2017), whereas those used for stone play by geladas (*Theropithecus gelada*) are not (Cangiano and Palagi 2020). Depending on the functions of such play, this could provide another example of convergence to a common function from play derived from different origins. What is not yet known is whether the neural circuits that produce and regulate social play are the same as those involved in play with objects or solo locomotor-rotational behaviour, nor is it known whether similar mechanisms are involved in any types of play across other vertebrate taxa. Clearly, there is convergence in complexity, and possible functions, in some types of play displayed by birds compared to mammals (Kaplan 2020), but whether this functional convergence also involves comparable mechanisms remains to be determined. Comparing mechanisms and functions of play between vertebrates and invertebrate phyla creates even greater challenges.

Even though we know so much more about play now than we did at the time of publication of Fagen's (1981) seminal book, the core challenge remains the same. Detailed studies of different kinds of play and forms of communication in social play across a larger sample of species spanning a wider phylogenetic spectrum are needed. The research progress made in understanding play fighting in a limited range of mammalian taxa provides a model for what is needed to understand the phenomenology of play more generally and thus identify the key causal and functional questions to pursue.

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PART 3

Complexities and Interactions

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17

WHAT IS COOPERATION, AND WHY DOES IT HAPPEN?

Amanda R. Ridley

Cooperation is a behaviour that permeates our everyday lives. Humans tend to live in societies and regularly interact with one another in a way that has led to us being considered not just cooperative, but super-cooperators (Nowak, 2006). Our ability to trade skills and ideas with one another is arguably what has led to significant technological advances (Horan, Bulte, & Shogren, 2005). Task partitioning, where individuals trade skills with one another such that products are produced more efficiently than if done individually, is extremely common in human societies. Animal analogs of this are eusocial insects such as bees, ants and termites, where individuals specialise on particular tasks such as mound/hive construction, care of young, food acquisition, or resource defence (Robinson, 1992). The remarkable architectural feats of humans, the huge communal nests of sociable weavers (*Philetairus socius*), and the robust, ventilated mounds built by termites are examples of the benefits of cooperation – many of these structures are unlikely to have been successfully built by individuals working alone, at least not within the same timeframes achieved compared to individuals working together. Cooperation is thus a topic that we (as a highly cooperative species) tend to be naturally interested in, because cooperation is at the core of our everyday lives and can at times turn into conflict: it is this delicate balance that is important to understand and maintain for individuals to continue to benefit from cooperation.

Broadly defined, cooperation is an action that an individual invests in (at some level of cost to itself), that benefits another individual. The action can also benefit the initiator of cooperation, either immediately or in the longer term. For example, the concept of reciprocity suggests that an individual that receives help now may in return help the individual that helped them at some future time (Trivers, 1971; Taborsky, Frommen, & Riehl, 2016a). Cooperation can take many forms, but it can be considered different from social or colonial behaviour. In the latter two, individuals may exist together in groups (e.g., for the benefits gained from predator dilution, or due to clumping around a desired resource (Lehtonen & Jaatinen, 2016)), but do not necessarily cooperate with one another. One type of cooperation that has captured a lot of research interest is cooperative breeding. This behaviour, where reproductively mature individuals may forgo their own breeding attempts (temporarily or permanently) and instead help to raise the young of others, has received much attention because it appears (at least at face value) to not fit well within the Darwinian framework of evolution. In writing *On The Origin of Species*, Charles Darwin suggested that natural selection would never produce an individual that incurs a cost on itself for the sake of others, suggesting that 'natural selection acts solely by and for the good of each'. Thus, much research has focussed on explaining how cooperation has evolved and can be stable over time despite it being a behaviour that incurs an immediate (and potentially longer term) cost to the cooperator. Indeed, despite decades of research

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on the topic, understanding cooperation is still identified as one of the top evolutionary challenges scientists will face in the coming decades (Pennisi 2005). Because cooperative breeding implies considerable cost to the helper (in terms of delayed reproduction as well as the cost of help), I will focus on this type of cooperation for much of the chapter.

Cooperation in humans and other animals: same or different?

Cooperation is a key aspect of human society that influences many aspects of our day-to-day lives, including politics, education, travel, trade, innovation, health care and technological advances. The benefits of human cooperation are so pervasive that they are at the core of many political and economic decisions: a literature search of cooperation in human societies returns over 178,000 peer-reviewed publications. The benefits of human cooperation are many and can regularly be seen in the humanitarian response to wide-scale events that affect large areas, such as natural disasters (hurricanes, large-scale volcanic eruptions) and global pandemics. Organizations such as the International Red Cross, *Médecins sans frontières* and others are examples of the human tendency to help others in need at a cost to oneself. Indeed, since the emergence of covid-19 as a global pandemic the importance of cooperation on both a local and broader level has been highlighted – lockdowns, social distancing and newly introduced health measures are only effective if a certain percentage of society cooperates and adheres to the rules (Powell & Meyers, 2021). Recent research has suggested that the effectiveness of the response to a pandemic threat can be increased if pandemics are viewed as a global public good (Brown & Susskind, 2020) where cooperation is key to maximize the common good (Powell & Meyers, 2021).

Cooperation also persists in many non-human animals and has been intensely researched for many decades. While the principles of cooperative research in animal and human societies tend to be the same including (a) how cooperation balances or offsets conflict (De Dreu & Gross, 2019; Wilczynski & Brosnan, 2021), and (b) what the benefits and cost of investing in cooperation are, there are also a number of differences. Some authors have previously opined that animal societies have limited evidence for cooperation compared to humans, stating that cooperation in animals is mainly limited to relatives, there is limited evidence for task partitioning or division of labour, no large-scale conflict, limited communication, and the weak or sick must fend for themselves (Boyd & Richerson, 2009). Some of these assumptions may be attributed to the familiarity effect: we tend to know less about other animal societies than we do about human societies. Recent research has revealed that more than 25% of cooperation among animals is between non-relatives (Riehl, 2013; Taborsky, Frommen, & Riehl, 2016a). Therefore, cooperation in animals cannot always be attributed to kin selection (see Table 17.1 for a definition of kin selection). While there is debatably little to be gained from finding direct analogs of key aspects of human cooperation in animals, there is arguably a lot that can be gained from finding common themes that can explain cooperation generally, and when cooperation may cease to be beneficial or turn into conflict. The recognition that human cooperation research can provide useful insights into cooperation research in other animals and vice versa can be illustrated by recent volumes that have involved debates regarding patterns of intergroup conflict in animals and humans (see De Dreu & Gross, 2019 and the associated commentaries on this review), and books on cooperation in both human and non-human animals (Wilczynski & Brosnan, 2021).

The kin selection debate

In many species, the individuals that are observed in cooperative interactions are related to one another. This naturally leads to the idea that cooperation must occur through the indirect genetic benefits individuals gain from helping kin. In order for this to be true, individuals should only help relatives when there are barriers to their own independent reproduction, since usually individuals can pass on more genes to the next generation by raising their own offspring than raising the young

Table 17.1 Definitions of terms commonly used in cooperative research.

Term	*Definition*
Cooperation	Two or more individuals acting or working together for some mutual benefit.
Altruism	A behaviour by an individual that increases the fitness of the recipient, at a cost to the fitness of the actor.
Reciprocal altruism	A behaviour by an individual that is initially costly to the actor but beneficial to the receiver, with the expectation that the receiver will return a benefit in the future.
By-product mutualism	When individuals cooperate because it is of their own individual benefit to do so, and the benefits that other individuals in the interaction receive arise as a by-product of individual benefits.
Kin selection	The process whereby traits become more common in successive generations as a consequence of the interactions among individuals who share common ancestry. Kin selection occurs when individuals direct beneficial behaviours more often to kin than non-kin.
Delayed dispersal	When individuals delay dispersal from their natal territory or group beyond the time that they reach sexual maturity.
Bet-hedging	A strategy whereby individuals may suffer decreased fitness under typical conditions as a trade-off for maintaining (or increasing) fitness under stressful conditions.
Costly signalling and the handicap principle	When a behaviour is costly, such as cooperative behaviour, individuals may invest in this behaviour as a signal of quality that leads to some benefit, such as reproductive opportunities. A costly trait reduces survival, and only high-quality individuals can afford handicaps. Therefore, the handicap acts as an indicator of quality and must be costly to guarantee that the signal is honest.

of genetic relatives (Hamilton, 1964). Several studies have revealed this to be the case, the classic example being white-fronted bee-eaters *Merops bullockoides* (Emlen & Wrege, 1988). In this species, most mature individuals initially attempt to breed. However, some of these breeding attempts fail. When this happens, individuals then go and help at the nest of others at the breeding colony, but these nests are more likely to be the nests of relatives than non-relatives. Importantly, individuals were more likely to help at the nest of close relatives than distant relatives, suggesting fine-scale kin preferences (Emlen & Wrege, 1988). Since Emlen & Wrege's research, many more studies have confirmed this kin selection trend in cooperative behaviour, including experimental kin choice studies (Russell & Hatchwell, 2001). These experimental studies provide convincing evidence of kin selection as an important factor influencing cooperative breeding behaviour in some species.

However, the idea that cooperation primarily occurs via kin selection may be misguided in some cases – as in, the idea has become so widely accepted that sometimes kin selection is assumed to explain patterns of observed cooperative behaviour, despite alternative explanations being possible. For example, when there are barriers to dispersal, individuals may end up helping their relatives as a by-product of limited dispersal options. Note that this is not to say that kin selection is NOT the main factor promoting cooperative breeding in some species. However, the presence of individuals helping kin doesn't necessarily imply kin selection. A better way to prove kin selection would be to show that when an individual is given a choice between helping a relative and a non-relative, that they choose the relative. In addition, for this to be convincing evidence of kin selection, their relative should not be simply the closest option for help (due to short-distance dispersal), or the easiest option for help. It is for these reasons that experimental studies such as the kin choice experiment conducted by Russell & Hatchwell (2001) are so helpful for understanding cooperative breeding behaviour, because they help to resolve the role of kin selection. In Russell & Hatchwell's 2001 kin selection study on long-tailed tits (*Aegithalos caudatus*), observations were made of patterns of helping behaviour by individuals whose own breeding attempts had failed. A remarkable 94% of failed breeders went to help at the nest of a relative, and most of those chose to help at the nest of a first-order relative rather than a second-order relative (Russell & Hatchwell, 2001). To rule out the possibility of kin-directed helping simply occurring because kin were closer to the potential helper at the time their own nest failed, Russell & Hatchwell (2001) experimentally manipulated failed breeder status for individuals whose nesting area was equidistant between the active nests of relatives versus non-relatives. They found that failed breeders were still more likely to help at the nest of a relative than a non-relative even when the distance between the two choices was the same.

Recent theoretical modelling of cooperation has revealed that non-kin cooperation can be more stable than kin-based cooperation in the long-term (Quiñones, Van Doorn, Pen, Weissing, & Taborsky, 2016), challenging some of the long-held beliefs regarding the importance of kin selection to the occurrence of cooperative behaviour. In some species, related helpers do not provide more help than unrelated helpers (Kaiser et al., 2019), and in some species helping non-relatives is common (Riehl, 2013; Taborsky, Frommen, & Riehl, 2016a). Indeed, it could be considered that all individuals that disperse from their natal territory and then help individuals in their new group are preferring non-relatives over relatives (assuming the members of their new group are not relatives); so much so that if the opportunity to help non-relatives versus relatives is calculated, helping non-relatives may be more common *relative to opportunity*. This is because when still present in the natal group, individuals tend to only have the opportunity to help relatives. Where there are barriers to dispersal (which can include the number of competitors in other groups, an individual's condition relative to competitors, ecological conditions, and limited territorial vacancies for example), the next best option may be to help those in your current group. This option doesn't always have to be a kin selection reason – individuals helping others can gain direct benefits from help, including forming social bonds with individuals that may become future coalition partners, gaining breeding experience, social queuing for dominance, defence of territorial resources, and greater survival probability living in a group compared to living alone or living in a lower quality habitat (Dyble, Houslay, Manser, & Clutton-Brock, 2019; Field & Leadbeater, 2016; Ridley, 2012; Ridley, Raihani & Nelson-Flower, 2008).

Direct benefits of cooperation

Direct benefits (as compared to the indirect benefits gained through kin selection) can fit well within the Darwinian framework of evolution because the cost of a cooperative behaviour is directly related to the benefit received. Human societies are a good example of cooperation among non-kin – non-kin cooperation is more the norm than the exception in humans (Silk & House, 2016). It therefore seems odd that there has been such a historical preoccupation with kin selection as a primary explanation for the evolution of cooperative behaviour in animal societies when we are surrounded by so many examples of non-kin cooperation. Natal philopatry – an individual's decision to delay dispersal and remain on the natal territory – creates a significant correlation between relatedness and helping behaviour, even if this is not the primary reason for the occurrence of helping behaviour. Given this correlation, how do we overcome this issue when studying cooperative behaivour? The easiest way to do this may be to look at causes of intra-individual variation in cooperative behaviour. For example, in some species, individuals that are about to disperse provide less help than they did during periods when they were not attempting dispersal (Zöttl, Chapuis, Freiburghaus, & Taborsky, 2013). Similarly, those that have a possibility of parentage in the brood may help more than those that do not. In some species, this effect of parentage uncertainty on cooperative care of young is so strong that females may strategically mate with multiple males to increase the amount of multi-male care given to her brood (Davies, Hartley, Hatchwell, & Langmore, 1996).

In mountain gorillas (*Gorilla beringei beringei*, Figure 17.1), there is considerable variation in the amount of time individuals invest in intergroup interactions (Mirville et al., 2018). Some individuals do not contribute at all, whereas others invest heavily, and may incur lethal or sub-lethal injuries as a result. Given the high potential cost of these intergroup interactions, we used individual participation data during 464 intergroup interactions over 13 years of observation of mountain gorillas at Volcanoes National Park, Rwanda. We found that participation in intergroup interactions was primarily driven by *individual* reproductive benefits (Mirville et al., 2018). Males with fewer mating opportunities participated in intergroup interactions less often, while female participation was related to the risk of infanticide – females were most likely to be involved in repelling lone mature males attempting to disperse into the group; successful dispersal of this type is related to higher levels of infanticide (Mirville et al., 2018). Although we included relatedness as a potential influencing factor in our analyses, we found no evidence of a relatedness effect on participation in territory defence. Rather, variation in investment in intergroup interactions at the individual level could best be explained by the direct benefits individuals would receive by participating. Thus, a closer look at cooperative breeding behaviour, where the causes of individual variation in contributions to care are considered, may best elucidate the relative importance of direct versus indirect benefits on cooperation, and remove the automatic kin-helping correlation that tends to arise when individuals delay dispersal. An increasing number of studies are investigating these patterns (Taborsky, Frommen, & Riehl, 2016b), and as a result, the importance of direct fitness benefits for the occurrence of cooperative behaviour is becoming more prominent.

Traditionally, research into the benefits of cooperation in animal groups has looked at the relationship between cooperation and life history parameters such as reproductive success, survival and individual state (Koenig & Dickinson, 2016). However, recent research has taken a closer look at

Figure 17.1 Two silverback mountain gorillas prior to an intergroup interaction. Intergroup interactions in mountain gorillas can be peaceful or aggressive, but not all group members contribute to interactions – participation is based on the potential benefits that can be gained from the interaction.

Photo courtesy of Melanie Mirville, Dian Fossey Gorilla Fund.

broader associations between cooperation and cognition, and cooperation and adaptation to highly variable climates. I will focus more on these broader relationships below.

The relationship between cooperation and cognition

In broad terms, cognition is defined as the way an animal receives, processes, retains, and acts (or not) on the information it receives from its surrounding environment (Shettleworth, 2009). Cognition is thus extremely important and can determine an individual's ability to successfully invade new environments (reviewed by Szabo, Damas-Moreira, & Whiting, 2020), or adapt to changing environmental conditions (Soravia, Ashton, Thornton, & Ridley, 2021). For several decades, the social brain hypothesis has been an important concept relating sociality to cognition. The social brain hypothesis predicts that individuals living in larger groups will face a greater complexity of social interactions, thus leading to selection for larger brains. Convincing evidence for this idea has come in the form of positive correlations between neocortex size and group size in primates (Dunbar, 1995), and positive correlations between group size and social complexity (but see Morrison, Eckardt, Stoinski, & Brent, 2020). However, there has been considerable debate over these results, with some arguing that brain size is not necessarily directly related to cognition (Ashton, Thornton, & Ridley, 2018; Healy & Rowe, 2013). To overcome these potential issues, another way to measure the relationship between cognition and sociality may be to measure intraspecific differences in cognition.

We investigated the causes of individual variation in cognition in the cooperatively breeding Western Australian magpie (*Gymnorhina tibicen dorsalis*). We conducted four different cognitive tests (associative learning, reversal learning, inhibitory control and spatial memory) on adult magpies in groups varying in size from 3–12 individuals (Figure 17.2). We found that individuals in larger groups had higher cognitive performance than individuals in smaller groups, providing support for the social intelligence hypothesis (Ashton, Ridley, Edwards, & Thornton, 2018) and thus highlighting a cognition benefit of cooperation. However, a potential issue with this result is that magpies are a long-lived species (they can live up to 25 years in the wild), and we were testing their cognition relative to

Figure 17.2 A Western Australian magpie interacting with a cognitive task. To measure cognition in relation to sociality, each individual is observed interacting with a series of cognitive tasks when other group members are not present within 10m.

Photo courtesy of Joseph Sollis.

their *current* group size, not their historical group size. Given that some of the individuals tested were nearly 20 years old, they may have historically been in smaller groups than the one they were in when we tested them (Ashton, Ridley, & Thornton, 2019). To address this potential confound, we looked at the ontogeny of cognitive performance. We tested fledglings from groups of known size (on the same cognitive tasks listed for adults above) and tracked their cognitive performance as they developed. We found that fledglings from large groups had significantly higher cognitive performance than fledglings from smaller groups by the time they were one year old (Ashton, Ridley, Edwards & Thornton, 2018), providing convincing evidence for the social intelligence hypothesis. Despite this convincing evidence, there remain some issues we need to resolve to further confirm the cognition–cooperation relationship; namely – we found a relationship between group size and cognition, NOT cooperation and cognition. What we now need to determine is what aspect of group size is related to cognition? Is it the complexity or frequency of social interactions (including communication), is it the level of cooperation in the group, or is it something else? Previous research has indicated that cooperative species tend to have a greater complexity of social interactions than non-cooperative species, including complex communication, negotiation and reciprocity interactions (Freeberg, Gentry, Sieving & Lucas, 2019; Quiñones et al., 2016; Taborsky et al., 2016a), which has often led to the assumption that cooperation is related to cognition. This remains an intriguing link that is oft assumed but yet to be fully proven.

Historically, group size has been considered a good indicator of levels of cooperation and social complexity (Koenig & Dickinson, 2016; Morrison et al., 2020). However, due to the presence of effects such as load-lightening (where an increase in group size leads to each individual contributing less, as is the case during intergroup interaction in mountain gorillas (Mirville et al., 2018)), there is increasing recognition that group size may be too simplistic a measure of cooperation. This has led to an increase in research into how best to measure social complexity, to better understand the complexities of cooperative breeding behaviour (Bergman & Beehner, 2015). These are important measures to gain since they directly impact our understanding of the benefits of cooperation relative to the costs. For example, if cooperation is related to cognition, as suggested in our research on Western Australian magpies, what benefit does this bring? Our research found that females with higher cognitive performance successfully raised more young each breeding season (Ashton, Ridley, Edwards, & Thornton, 2018), implying an evolutionary benefit of cognition that is influenced by group-living behaviour. To determine if this is a cognition benefit of cooperation *per se* or group-living behaviour, the next step is to compare cognition between individuals in groups of the same size that vary in their level of cooperative behaviour.

The relationship between cooperation and environmental conditions

One hypothesis for the evolution of cooperation is that it evolved as a strategy that allowed species to either invade or persist in habitats with typically harsh or highly variable environmental conditions. The idea behind this hypothesis is that environmental factors that may prevent pair-breeding in some years (e.g., severe drought leading to low availability of resources) might not inhibit breeding in cooperatively breeding groups as much, since groups have multiple adults able to find food for group young and may be able to defend access to limited resources more effectively than a breeding pair or lone individual. Cooperative breeding can thus be considered a bet-hedging strategy (see Table 17.1 for a definition of bet-hedging) that reduces the variance in reproductive success caused by variable environmental conditions (Rubenstein, 2011). If this hypothesis is correct it would allow cooperatively breeding species to evolve in highly variable environments (Rubenstein & Lovette, 2007), colonise such environments (Cornwallis et al., 2017), or prevent extinction during harsh conditions (Griesser, Drobniak, Nakagawa, & Botero, 2017). Given that many habitats are expected to undergo rapid environmental change due to climate change impacts, understanding the importance of cooperation as an adaptation to environmental conditions may help us to predict the impact of climate change on species with different breeding systems (Firman, Rubenstein, Moran, Rowe, & Buzatto, 2020).

Phylogenetic analyses of both mammals and birds have confirmed theoretical predictions that cooperative breeding tended to evolve in highly variable habitats (Firman et al., 2020; Griesser et al., 2017). In addition, several long-term research studies have used years of demographic and environmental data to investigate this relationship. In white-browed sparrow-weavers (*Plocepasser mahali*), helpers reduce female reproductive variance relative to environmental conditions (Capilla-Lasheras, Harrison, Wood, Wilson, & Young, 2021), while in meerkats (*Suricata suricatta*) the effects of low rainfall on dominant female reproduction are mitigated by the increase in helper number in large groups (Groenewoud & Clutton-Brock, 2021). However, in other cooperatively breeding species there is limited support for the bet-hedging hypothesis. For example, in acorn woodpeckers (*Melanerpes formicivorous*) there was marginal evidence for cooperation buffering against environmental effects (Koenig & Walters, 2015), while in superb starlings (*Lamprotornis superbus*), sociable weavers and pied babblers (*Turdoides bicolor*), there was no relationship between group size or the presence of helpers on the annual variance in reproductive success or offspring survival and development relative to environmental conditions (Bourne, Cunningham, Spottiswoode, & Ridley, 2020a, 2020b; D'Amelio et al., 2022; Guindre-Parker & Rubenstein, 2020).

Support for the hypothesis of cooperation as a bet-hedging strategy to reduce the impacts of environmental conditions on survival and reproductive success is thus equivocal. There are several potential reasons for this: (a) we do not have enough studies with a long enough time series of data to be able to robustly determine patterns of variation in reproductive success in relation to environmental conditions or (b) there are multiple factors that promote cooperative behaviour in relation to environmental conditions, and these differ between species. That environmental conditions are unlikely to be a consistent rule that explains cooperative behaviour can be seen by the fact that there are numerous non-cooperative species that occupy the same habitats that cooperative species do. To address this issue of cooperation occurring in both benign and harsh environments, and stable and fluctuating environments, Shen et al. (2017) developed the dual benefits framework for the evolution of cooperative breeding. This framework proposes two routes for the evolution of cooperation: species in spatially variable environments where resource defence benefits favour group-living, and species in temporally variable environments, where individuals gain direct benefits through collective action. Although a relatively recent framework, empirical evidence in support of this hypothesis is accumulating, with sociality being favoured under varying environmental conditions in the burying beetle *Nicrophorous nepalensis* (Liu et al., 2020) and delayed dispersal being affected by a range of ecological and social factors in the pied babbler (Nelson-Flower, Wiley, Flower, & Ridley, 2018).

Despite equivocal support for the ability of cooperation to buffer individuals against the effects of environmental conditions, for those species where we do have enough long-term demographic data to see how reproductive success varies over time, we can develop population viability analyses to determine the potential impact of increasing temperatures on population persistence. As an example, in the pied babbler (a cooperatively breeding passerine endemic to the semi-arid Kalahari, Figure 17.3), we used 17 years of demographic data to determine that pied babbler reproduction was negatively affected by low rainfall and high temperature conditions, irrespective of group size (Bourne et al., 2020a, 2020b). This resulted in population declines during years of low rainfall and above average temperatures. Using the expected increase in temperature and drought conditions due to climate change, we ran scenarios where we increased the annual frequency of both drought and above average temperature events. The output of these viability analyses was a high probability of population decline and increased likelihood of local extinction for the pied babbler due to the predicted impacts of climate change (Ridley, Wiley, Bourne, Cunningham, & Nelson-Flower, 2021). Thus, in pied babblers, where group size does not buffer individuals against environmental extremes, the species faces a high probability of disappearing from large parts of its current range in the coming decades. Population viability analyses for cooperative species should therefore consider the effect

Figure 17.3 Pied babblers displaying heat stress. The bill gaping behaviour typical during heat stress makes foraging less efficient, and results in less food provisioned to young.

Photo courtesy of Nick Pattinson.

of cooperation on reproductive success under varying environmental conditions in order to obtain accurate estimates of likely future population status – this is particularly important for threatened species, or species currently experiencing population decline.

Conclusions

How and why cooperation exists is still considered one of the major evolutionary questions we face (Pennisi, 2005), since it explains the major transition from unicellular to multicellular life, and from solitary living to sharing of specialized skills in large, complex societies. Some common themes to explain the evolution of cooperation, such as kin selection and ecological conditions, have persisted for many decades. Yet the way we collect evidence for these theories is changing and is generating new and fascinating empirical data. By looking at individual variation in contributions to help within a group for example, we can tease apart indirect kin selection benefits from other, direct benefits of cooperative behaviour. In addition, by considering social complexity rather than simply group size, we may better understand the benefits and costs of cooperative behaviour. Long-term data can also help disentangle the causes of cooperative behaviour relative to the benefits an individual receives over their lifetime. For example, the long-term mountain gorilla data on intergroup interactions revealed participation was based mainly on the risk of infanticide for females, and reproductive opportunities for males, with no evidence of an impact of relatedness (Mirville et al., 2018). In addition, our long-term research on pied babblers revealed no support for the hypothesis that cooperation evolved as a strategy to buffer individuals against environmental extremes – with group size not moderating the impacts of high temperatures and drought on the development and survival of young or adults ((Bourne, Cunningham, Spottiswoode, & Ridley, 2020a, 2020b) While cooperation is extremely complex and can be influenced by multiple factors, there are some common themes that have emerged that can explain the evolution of cooperation, including direct and indirect benefits, and environmental conditions. I suggest there are two main ways to move the field of cooperative research forward in new and exciting directions: (a) greater collaboration between researchers working on human and non-human animal cooperation and (b) where possible, controlled experiments to control for confounding factors that may be influencing cooperative behaviour (such as kin selection versus delayed dispersal explanations for the occurrence of cooperative behaviour).

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18

CULTURAL BEHAVIOUR IN CETACEANS

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Introduction

Whales and dolphins (order *Cetacea*) form a diverse group of approximately 90 species, which inhabit not only the full range of our planet's oceanic environments from the tropics to the polar oceans but also some of its great rivers. The challenges of studying these inaccessible animals mean that their cognitive and perceptual abilities, behaviours, and social structures are poorly understood, and indeed in many species remain completely unknown. However, research effort over the past 50 years, and especially in the last two decades, has begun to pull back the curtain as we develop integrated knowledge of these features with their life histories, ecologies, and phylogenies. Neuroanatomical and laboratory studies have confirmed that these large-brained mammals possess complex cognitive and communicative abilities (Marino et al., 2007), including capacities for social learning (Herman, 2002; Janik, 2014). Cetacean brains appear to have coevolved with complex social structures and rich behavioural repertoires comparable to those of primates and elephants (Connor et al., 1998). Furthermore, for some species extensive fieldwork has established that individual populations may exhibit distinctive enduring traditions (e.g. vocal dialects in killer whales, migration routes in humpback whales) as well as passing 'fads' of socially transmitted behaviour (e.g. tail-walking in bottlenose dolphins, dead-salmon pushing in killer whales), which may productively be described as cultural (Whitehead and Rendell, 2015).

Such descriptions rely on a broad concept of culture, which we also adopt, that identifies it as a 'second inheritance system' in contrast to genetic inheritance (Whiten, 2021). Following Laland and Hoppitt (2003), culture may be defined as "those group-typical behaviour patterns shared by members of a community that rely on socially learned and transmitted information." As we will see below, socially learned and shared behaviours are important in part because they permit fast and flexible adaptive responses to changes in the environment, and the exploitation of novel ecological niches, but it is important to note both the existence of maladaptive variants (Laland and Janik, 2006), and the fact that cultural conservatism can impede adaptive responses to environmental change. The existence of culture (in this broad sense) has been demonstrated for a wide range of mammals, birds, fish and insects (Whiten, 2021), but cetaceans are distinguished alongside primates (Whiten et al., 1999) and some avian species (Aplin, 2019) by the wide range of domains across which their cultures extend: communication, migration, prey preference, hunting and foraging strategies, habitat use, movement, social rituals, and play. It is, as Whitehead and Rendell (2015) express, vital, in the sense that it seems unlikely that individuals in these species could develop into fully participating and reproductive adult members of their society without appropriate cultural inputs.

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Figure 18.1 Intense socialising in a sperm whale social unit © Whitehead Lab

Considerable care must be taken over claims for culture in nonhuman animals. Shared behaviours and community-wide differences may arise through mechanisms other than social learning. Rigorously demonstrating the existence of social learning is most convincingly achieved through the use of controlled behavioural experiments, whether with captive or wild populations (Whiten, 2021). Such experiments may also allow hypotheses to be tested on the form of cultural transmission (e.g. vertically, from parents to offspring, or horizontally, among individuals of the same generation) and the existence of 'transmission biases' (e.g. the tendency to learn from dominant individuals). For cetaceans, however, such experiments are subject to substantial practical and ethical constraints. Consequently much of the evidence in support of the existence of culture and the underlying process of social learning is indirect, coming from long-term field observations of a variety of species, but a body of work on action and vocal imitation in smaller captive cetaceans also provides direct evidence for the mechanisms of cultural transmission. Outside the laboratory, the existence of behavioural diversity has to be considered alongside genetic or environmental variation, to assess the extent to which such diversity is caused by genotype differences (and hence may arise without social learning) or by ecological factors such as the presence of a particular prey-species about which animals learn for themselves. The latter consideration is double-edged: since responding to local ecology is thought to be a major adaptive explanation for the evolution of culture in the first place, we expect to find the very correlation that makes it difficult to definitively prove cultural inheritance as a causal factor (Laland and Janik, 2006). Nonetheless, some features allow us to be more confident in the case of cetaceans. First, the existence of behavioural variation in sympatry is strong evidence for these behaviours being cultural. Strong evidence in support of culture also arises fortuitously on occasions when behaviours change rapidly across a whole community on spatial and temporal scales that we can observe directly and no mechanism other than social learning is feasible. Here we can refer to cultural evolution and even revolution (Noad et al., 2000).

As we discuss below, the study of cetacean cultures is providing valuable evidence relevant to current broader debates in cultural evolution: these include comparative questions about the evolution of culture and the cognitive mechanisms that underpin its various forms, and the reach of gene-culture coevolution (interactions between cultural and genetic evolution) across the animal kingdom (Whitehead et al., 2019). Whales and dolphins have thus become important in comparative work in this area. However, before a necessarily brief survey of the evidence of cultural behaviour, followed by specific focus on two case studies, we provide some biological context by describing relevant characteristics of cetaceans that have arisen since their ancestors entered the oceans around 50 million years ago (mya).

Cultural Predators in the Ocean

Cetaceans comprise the largest, most diverse and most cosmopolitan group of marine mammals. Their evolution from the cetartiodactyla (even-toed ungulates) involved major anatomical and physiological adaptations for full-time aquatic living and eventual divergence into two clades around 35 mya: the odontocetes (toothed whales) and the mysticetes (baleen whales). Odontocetes (a group including all dolphins and porpoises) developed the ability to echolocate, producing high amplitude broadband clicks to allow the detection and hunting of prey in deep and hence dark waters: sperm whales, for example, feed predominantly on various cephalopods which they catch during dives lasting 30–45 min, typically to a depth of 300–800 m (Whitehead, 2003). In the mysticetes, teeth were replaced by sieve-like plates called baleen, enabling highly efficient systems of skim and gulp feeding on the vast schools of krill and small fish living closer to the ocean surface.

One result of returning to aquatic habitats which has important implications for culture is the evolution of a consistently high level of maternal investment in offspring. Female cetaceans produce a single large and precocial calf after a prolonged gestation and birth is followed by lengthy lactation and maturation periods, leading to long interbirth intervals (Whitehead and Mann, 2000). The time mother and calf spend together permits extended social learning and therefore facilitates the vertical transmission of community-wide behaviours and knowledge in all cultural domains, from bottlenose dolphin foraging techniques (Mann and Sargeant, 2003) to humpback whale migration routes (Baker et al., 1990). The resulting strong mother-calf bond, which can be lifelong in some odontocete species, becomes the "cornerstone of cetacean societies" (Rendell et al., 2019), in part determining its structure. In turn, the type of social structure exhibited by a population strongly affects the ways in which cultural behaviours are maintained and diffuse within it.

For all cetaceans, the fact that water transmits sound much better than it does light has led to evolutionary emphasis on acoustic rather than visual forms of sensory biology and communication. Together with social complexity (Freeberg et al., 2012), the functional importance of sound in their sensory biology (both passive and active) may partially explain the evolution of vocal learning in cetaceans to an extent matched only by birds, and within the primates, only by humans (Janik, 2014).

The Reach of Culture in the Oceans

Mysticetes

The primary social relationship in mysticetes is that between mothers and calves, but this bond appears not to persist beyond weaning at 5–7 months in most species (Whitehead and Mann, 2000). Maternally directed learning is likely responsible for trans-generational fidelity to migratory routes and destinations, which has been inferred in humpback (Baker et al., 1990) and southern right whales (Carroll et al., 2015) from the geographic structure of matrilineal mitochondrial DNA (mtDNA) variation. Beyond this, mysticete societies are generally homogenous, mainly comprising "small, unstable groups" (Clapham, 2000). Longer-lasting associations have however been observed between pairs and trios of humpback whales on feeding grounds in the Gulf of Maine, including groups that re-associate from one year to the next (Weinrich, 2011).

Tighter social connections have also been observed within some groups of humpback whales in Southeast Alaskan waters, where individuals may play specialized roles in the teamwork required for bubble-net feeding on herring; other groups specialize on independent krill feeding and have a looser social structure (Wray et al., 2021). Compelling evidence for culture comes from observations in the Gulf of Maine of the diffusion of 'lobtail feeding', a modification of bubble-net feeding first seen used by a single humpback whale in 1980. Network-based diffusion analysis of data collected 1980–2007 revealed the way in which lobtail-feeding spread rapidly, preferentially and 'horizontally' among humpbacks with greater social connections, becoming a community-wide tradition and implying social transmission (Allen et al., 2013). Other community-wide specialized and distinctive foraging techniques include trap feeding in humpbacks (McMillan et al., 2019) and tread-water feeding in Bryde whales (Iwata et al., 2017).

Humpback whale song presents a further widely accepted example of cetacean culture. It exhibits synchronous and population-wide changes that are too fast to be accounted for by genetic or environmental changes and can only result from social learning (Garland et al., 2011). Although this is the best-studied and most complex example of mysticete song, the global long-term trends observed in blue whale song frequency (McDonald et al., 2009) and the annual replacement of shared song types in bowhead whales (Stafford et al., 2018) are also suggestive of a role for social learning (though confirmation would require a more detailed knowledge of population structure). Furthermore, the complexity and variability in fin whale song is currently being explored: a detailed study of song in Hawai'ian waters has shown that individual animals use multiple song patterns, and hypothesized that cultural transmission from the west coast of the USA might explain a change in dominant song type (Helble et al., 2020).

Odontocetes

Toothed whales have widely diverse morphologies, life histories and social structures. In contrast with mysticetes, they share an extended lactation and weaning period of one to three years or more (Whitehead and Mann, 2000), which has a large impact on social structures and vertical cultural transmission. This extended period may be the general result of the development time demanded by higher encephalization (Barton and Capellini, 2011), but may also be a particular consequence of the requirement to acquire the social skills needed as adults in their more complex societies (Connor et al., 2000). Such a long period spent together is associated with prolonged, sometimes lifelong, bonding between mothers and their calves (both male and female in some species), delayed age of sexual maturity, and complex societies in which modularity correlates loosely with body size (Rendell et al., 2019). In addition, odontocetes offer a nonhuman example of menopause (Ellis et al., 2018). Here culture has a possible co-evolutionary role, where the inclusive fitness benefits to the group of the ecological knowledge possessed by older females outweigh the direct fitness costs to the individual of the cessation of reproduction in response to inter-generational competition (Croft et al., 2017).

In general, smaller odontocetes live in geographically or socially defined communities within which we see constantly changing patterns of association creating a fission-fusion dynamic on a range of temporal and spatial scales (Gowans et al., 2007) and, for some populations at least of the well-studied bottlenose dolphin, enduring relationships between individuals (Connor et al., 2000). By comparison, the social networks of larger odontocetes such as killer and sperm whales are distinguished by a higher degree of matrilineality and a tendency towards hierarchical (multi-levelled) organization (Gero and Rendell, 2015). The stability of matrilineal groups in the larger toothed whales makes shared behavioural traditions easier to identify as culture, particularly where mating takes place between matrilines and/or more than one matriline with different behavioural traditions inhabits the same environment.

As in the mysticetes, the existence and transmission of diverse foraging techniques provides strong evidence for culture in the toothed whales. In the Shark Bay (Western Australia) population of bottlenose dolphins, foraging tactics include 'beaching', 'snacking' and 'sponging', the carrying of basket sponges on the beak to rub over the sea floor when hunting in deep water channels (Smolker et al., 1997; Mann and Sargeant, 2003). Social learning is hard to prove for wild populations due to the uncontrolled presence of multiple contributing factors including variable habitats, but Sargeant and Mann (2009) used multiple regression techniques to distinguish among these factors, showing that for three foraging types (including sponging) variation in maternal foraging predicted variation in calf behaviour. This evidence for vertical transmission of sponging is strongly supported by an application of network-based diffusion analysis which demonstrated that its observed spread was best accounted for by a network based on mother-calf relationships rather than on other associations, ecological factors or genetic relatedness (Wild et al., 2019). It is further reinforced by mtDNA analyses in two distinct regions of Shark Bay which revealed that in both areas sponging is passed almost exclusively from mothers to calves (Krützen et al., 2005; Kopps et al., 2014); together these studies support the hypothesis that sponging is cultural under our definition. Such vertical transmission is the usual pathway for social learning in toothed whales, so the recent network analysis of the spread of 'shelling' by the Shark Bay dolphins, showing horizontal transmission of an innovative hunting strategy, is especially intriguing (Wild et al., 2020).

We turn now to the killer whale, which exists as several distinct 'ecotypes' whose populations display extreme conformity in many aspects of their behaviour: diet and foraging strategy, vocal and social behaviour, and social organization. For example, the fish-eating killer whales of the waters around Vancouver Island (British Columbia) live in hierarchical communities founded on extremely stable matrilineal groups containing individuals from up to four generations: members rarely leave for more than a few hours, and male and female offspring do not leave until the oldest matriarch dies, at which point the group may begin to split up (Baird, 2000). By comparison, the population of mammal-eating killer whales occupying the same region show a simpler and somewhat looser social structure (Baird and Whitehead, 2000).

Genetic and morphological differences between ecotypes, coupled with reproductive isolation, have led to proposals that killer whale ecotypes are undergoing incipient speciation (Riesch et al., 2012) or should already be classified as different species (Morin et al., 2010). Culture itself can play an important role in the speciation of sympatric groups due to social exclusivity ('xenophobia') inhibiting interactions among ecotypes (including mating) or the social transmission of innovative behaviours with fitness consequences (Riesch et al., 2012). These ecotypes present some of the best evidence for gene-culture co-evolution outside humans, where culturally transmitted foraging tactics lead to divergent diets and consequently divergent selection on genes coding for, among other things, various digestive enzymes (Foote et al., 2016).

The earliest and best evidence for cultural transmission in killer whales comes from their group-specific dialects of stereotyped calls. Different populations of the same ecotype sharing the same waters have their own stable dialects, and for the fish-eating killer whales off Pacific Canada this cultural variation extends still further, dividing the northern 'community' into three 'acoustic clans' with no shared call types (Ford, 1991). Even the repertoires of related matrilineal groups are somewhat distinct. The existence of mating between members of different clans shows that this mapping between relatedness and similarity of repertoire cannot be solely determined by genetics (Whitehead and Rendell, 2015). Further firm evidence for the conclusion that dialects are maintained by social learning comes from work on dialect change. Comparing call types from two matrilineal groups from the same acoustic clan, Deecke and colleagues (2000) showed that over a period of 12–13 years one call type stayed the same but the other evolved and diverged between the two groups. Such rapid dialect change cannot be under purely genetic control. The details of the changes reveal details of the underlying mechanism(s): in this case, the amount of inter-group divergence was lower than expected to result from cultural drift (mutational changes coupled with intra-group behavioural matching) alone, suggesting a degree of horizontal transmission between the matrilineal groups.

Social Learning Mechanisms

As we have seen, there is an abundance of indirect evidence that much behavioural diversity observed in groups of free-living cetaceans depends on social learning. Such cultural transmission could rely on any of a variety of social learning mechanisms, as discussed in Whitehead and Rendell (2015), from the simplest stimulus enhancement up to the more cognitively demanding imitative and emulative processes documented in humans and other primates (Whiten, 2021). We focus here on direct evidence for vocal and motor imitation stemming largely from work on captive odontocetes, and briefly assess the evidence for teaching in cetaceans.

Vocal imitation is a special case of vocal production learning likely to benefit social functions including individual and group recognition, mate attraction, and group cohesion, and said to occur "where the vocalizations themselves are modified in form as a result of experience with those of other individuals" (Janik and Slater, 1997). Vocal production learning is widespread among birds and possessed by humans and cetaceans, but rare in other mammalian groups. Captive bottlenose dolphins were shown decades ago to be able to imitate both previously unheard artificial sounds (Richards et al., 1984) and the individually distinctive 'signature whistles' of conspecifics (Richards, 1986); similar capacities have been found more recently in killer whales (Abramson et al., 2018) and belugas (Murayama et al., 2014). These laboratory findings have been put into social context during capture-release events in the Sarasota Bay (Florida) dolphin population, in which small groups held for a short time for health monitoring had their vocalizations recorded. During these events, dolphins mainly produced their own signature whistles, but when the group contained a mother-calf or male-male alliance pair one or both members of the pair also produced the signature whistle of the other member in around 25% of cases (King et al., 2013). Playback experiments with the Shark Bay dolphins have also demonstrated that signature whistles play a key role in the formation of cooperation-based associative concepts (King et al., 2021).

When it comes to motor actions, bottlenose dolphins are renowned for their synchronous behaviour, which plays an important role in the wild in regulating male-male alliances (Connor et al., 2006). Synchrony is a sign of the ability of one animal to copy the motor behaviour of another, and such capacities were explored in depth in work done at the Kewalo Basin facility in Honolulu from 1979–2004 (Herman, 2002). In one investigation two female dolphins were taught a 'copy' command, and then each one tested on its ability to copy an act performed by the other when given only this command. Herman reports that one dolphin successfully copied seven out of twelve familiar and two out of three novel behaviours, with the other dolphin a little less successful. In a replication attempt using two male dolphins (Bauer and Johnson, 1994) the copying of familiar behaviours (mimicry) was achieved at a level higher than that of chance, but novel behaviours were not reproduced. The copying abilities of dolphins were further explored in an experiment in which one animal was taught to copy familiar motor actions whilst blindfolded (Jaakkola et al., 2013). When the model was a human rather than another dolphin, the increased echolocating activity observed suggests intentional and flexible switching between copying strategies, supporting the interpretation that the dolphin possesses a 'concept' of imitation (Herman, 2002). Further strong evidence for imitation in odontocetes has been supplied for killer whales using the protocol described here for the tests on dolphins (Abramson et al., 2013); in this experiment all three subjects learned the 'copy' command very quickly, and proceeded to copy successfully both familiar and novel behaviours.

The capacities for motor imitation and mimicry implied by the results of these experiments are very likely involved in the cultural transmission of behaviours in the wild, including the specialized foraging techniques found in wild dolphin and killer whale populations (Whitehead and Rendell, 2015). When it comes to vertical transmission from adult to young, there is also compelling (though not yet thoroughly convincing) indirect evidence for active demonstration, scaffolding or teaching in cases including crater-feeding in the Atlantic spotted dolphin (Bender et al., 2009) and the intentional stranding of killer whales (Guinet and Bouvier, 2011).

Our review to this point has been necessarily lacking in details, because complete accounts of all these behaviours would require book-length treatment (Whitehead and Rendell, 2015), but we provide two case studies here, to describe more fully the kinds of observations that make the case for cetacean culture so compelling.

Case Studies

1. Humpback Whale Vocalizations: Evolution and Revolution

The cultural transmission of humpback whale song provides one of the most striking examples of broad-scale cultural transmission in the animal kingdom, rivalled only by humans. Male humpback whales sing a long, stereotyped, complex breeding display termed 'song' (Payne and McVay, 1971), composed of hierarchically organized 'song units'. Song functions in sexual selection but the exact function, whether it is directed at other males, females or both, is still debated (Herman, 2017). Within a population, all males sing the current arrangement of the song (termed 'song type'); hence there is strong cultural conformity to the current song norm (Payne et al., 1983; Payne and Payne, 1985). Each year, the song gradually evolves at all levels in the song hierarchy (Payne and Payne, 1985) and all males incorporate these changes into their song to maintain the observed conformity. Within an ocean basin songs are similar among populations but the level of similarity depends on the geographic distance between populations and also a time-transmission component (Payne and Guinee, 1983; Garland et al., 2011; Darling et al., 2019). Populations in different ocean basins sing different song types (Payne and Guinee, 1983); however, a different picture appears to be emerging in the Southern Hemisphere.

Two decades ago, a rapid and drastic form of song change (termed 'song revolution') was first documented (Noad et al., 2000). Song from the west Australian population located in the South Indian Ocean basin appeared in the east Australian population located in the South Pacific Ocean and replaced the existing song over the course of two years. The novel song type rapidly replaced the existing song, thus rapidly changing the cultural variant displayed in the population. Subsequent work has traced multiple song revolutions as a series of cultural waves spreading east across the western and central South Pacific region over the last two decades (e.g., Garland et al., 2017, 2011; Owen et al., 2019). This created the checkerboard pattern of behavioural variants at the decadal and ocean basin scale shown in Figure 18.2.

While this presents a clear example of cultural transmission at a vast scale, understanding how humpback whales rapidly learn a new song is challenging. Studying rare hybrid songs, where a whale was recorded singing new revolutionary song combined with current song has shown that singers segment their song as whole themes. A 'switch when similar rule' was also uncovered as singers would switch between the two different song types at the position in the song (the theme) with the highest similarity in arrangement and unit types (Garland et al., 2017). In between revolutions song complexity (indexed by the number and distribution of unit types) in the east Australian population increased as songs evolved, but decreased during revolutions, creating an oscillating pattern of complexity (Allen et al., 2018). These authors hypothesized that, given their complexity and the amount of novel song material required to be rapidly learnt during revolutions, revolutionary songs may represent an upper limit to song learning. There remain many further unknowns regarding song transmission and vocal learning in humpbacks; active areas of research include song ontogeny and the relationship between song performance and reproductive success which will be crucial to understanding adaptive benefits.

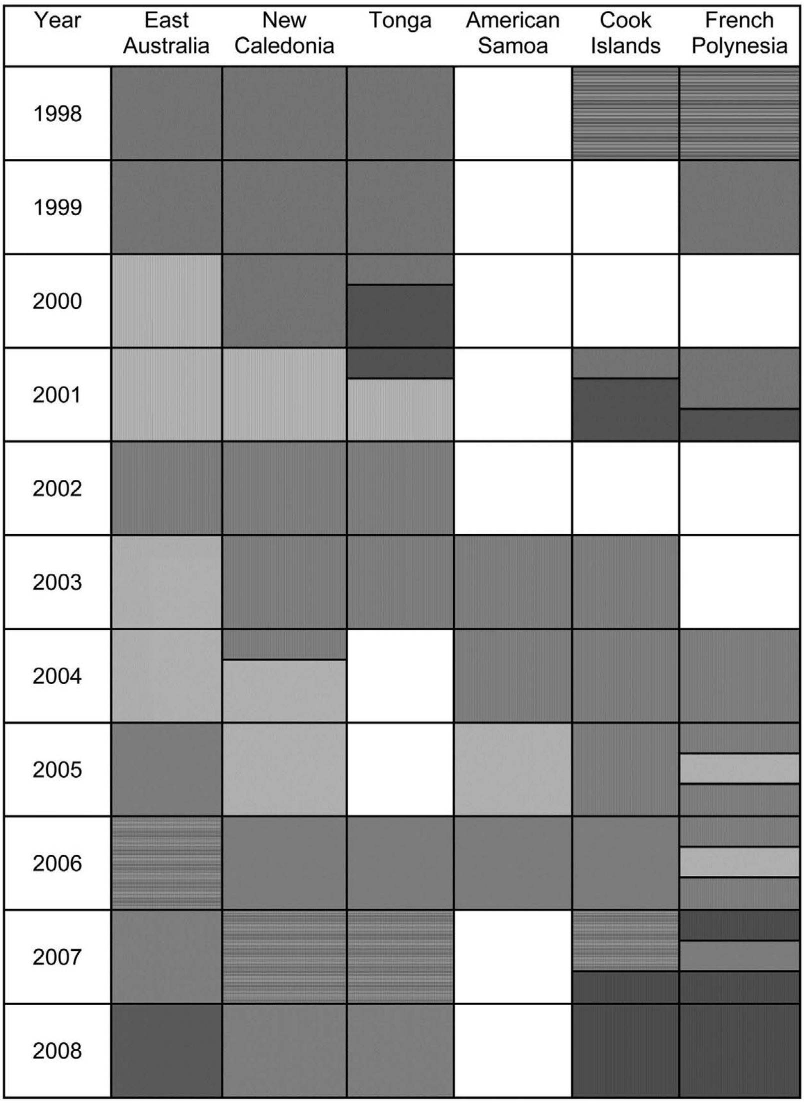

Figure 18.2 Song types identified in the South Pacific Region from 1998 to 2008. Populations are listed from west to east across the region. Each hatching style represents a distinct song type. Unpatterned cells represents no data available. Two patterns within a year/location indicate both song types were present (e.g. Tonga 2000). In these cases the seasons are broken into three periods (early, middle or late) to indicate when a new song type was recorded. Different shades of grey underneath the same hatching style represent evolutionary song change – minor modifications to the same general song type. Originally published in Garland et al. 2011.

2. Sperm Whale Codas and Clan Structure

Evidence for cultural variation in behaviour of sperm whales, the largest odontocete, has been derived principally from studies of their vocalizations. Sperm whale vocal behaviour is dominated by the production of the echolocation clicks that facilitate the whales' knowledge of their deep sea surroundings, but there has also been considerable focus on their production of stereotyped patterns of clicks, termed codas, which have been shown to be social in function (Whitehead, 2003).

The strongest evidence for cultural processes in sperm whales relates to dialect variation in the repertoires of these coda vocalizations. Initial studies of the coda repertoires of social groups in the waters around the Galápagos Islands showed that variation in repertoire occurred within populations and was correlated with matrilineal mtDNA (Whitehead et al., 1998). Subsequent detailed analysis of these repertoires and others from the wider Eastern Pacific including the waters off Ecuador and Chile showed that every social group recorded in the period 1985–1999 could be assigned to one of three vocal 'clans' based on shared coda repertoires (Rendell and Whitehead, 2003). The term 'clan' implies a common genealogy, and it is the case that there are marked differences in the frequencies of different mtDNA haplotypes (i.e. matrilineal lineages) across the different clans, but these patterns are not consistent with a simple genetic transmission hypothesis for explaining the dialect variation (Rendell et al., 2012). The sympatric occurrence of these dialect variations rules out an ecological explanation. Subsequent studies of dialect variation in other regions has revealed the existence of similarly sympatric vocal clans in the Eastern Caribbean (Gero et al., 2016), but in other areas there appears to be only a single dialect variant, for example in Japanese waters (Amano et al., 2014) and in the Mediterranean (Drouot et al., 2004) while in other regions apparent dialect boundaries can be identified (Amorim et al., 2020). Why some areas appear to have multiple variants and others not remains unknown, but there is evidence of large-scale population dynamics tied to these cultural variants around the Galápagos, where a period of apparent loss and then re-invasion of sperm whales coincided with the disappearance of two of the most abundant clans from the 1985–1999 study. In their place, two different clans were identified in studies conducted in 2013–2014, showing that the population turnover occurred along cultural lines (Cantor et al., 2016). Thus cultural variation appears to be a significant factor in the structure and dynamics of sperm whale populations globally.

One clue as to the reasons why there are multiple clans in some regions comes from data suggesting there is more to clan membership than just vocal dialect. Around the Galápagos there is evidence that although sympatric on scales of a few hundred kilometres, clans do show specific fine-scale habitat partitioning (Eguiguren et al., 2019) and apparently vary in the ways they use that habitat, leading to sometimes marked variation in feeding success between the clans (Whitehead and Rendell, 2004), with further evidence of consequent variation in reproductive success (Marcoux et al., 2007). Currently these variations are only described in the broadest terms and we await further information on the details of how clan membership links to other behavioural traits and to functional benefits, but it is becoming clear that the clan into which a sperm whale is born may determine a whole range of outcomes for that individual – where they will spend their lives, what habitats they may occupy, the foraging strategies they deploy, and the extent to which they will be vulnerable to ecological change, all of which appears to derive from cultural inheritance (Whitehead and Rendell, 2015).

Conclusion and Future Directions

We have seen that cetaceans offer a fascinating range of cultural behaviours in a group of mammals that has evolved to flourish in an environment vastly different from our own: it is remarkable to see the independent evolution of capacities for social learning (including vocal and action imitation), the menopause, and roles for horizontal and vertical cultural transmission in maintaining distinct and multi-patterned societies in near-identical environments. These examples of convergent evolution provide important opportunities to help explain the origins, and functional costs and benefits, of culture and its cognitive substrates in primates and other taxa.

The diverse forms of cetacean cultural evolution also offer significant models to be compared with primate and avian cultures in attempts to understand, for instance, how horizontal cultural transmission supplements gene-based adaptive evolution in allowing the spread of beneficial behaviours among unrelated individuals (e.g. Whitehead et al., 2021). The co-evolution of culture with nuclear and mitochondrial DNA is currently being investigated through modelling studies, which have highlighted the effects of culture on selection pressures, and the importance of gene-culture co-evolution for understanding population genetic structure and diversity, and speciation in cetaceans (Whitehead et al., 2019).

An understanding of the role culture plays in determining population dynamics may have important implications for the understanding of post-whaling population recovery, and should be included in future conservation protocols. For example, horizontal transmission may aid rapid, adaptive responses to anthropogenic climate change, but vertical transmission may impede such adaptation (Brakes et al., 2021).

Finally, future research into the acquisition and development of cultural behaviours in individual animals can further inform us about cognitive capacities such as memory and social learning. When integrated with knowledge of other behaviours and facets of life history (such as sociality and reproductive success), such research may tell us more about the evolutionary functions of behaviours, for example song, which have so far remained somewhat opaque not just in cetaceans but also in *Homo sapiens*.

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19

TOOL USE

Akane Nagano

What is tool use?

Historically, it was believed that tool use was one of the prerogatives of humankind, and that tool use was not done by other animals (Baber 2003). However, many studies—since 1830—have reported that nonhuman animals also use tools, both in the wild and in experimental settings (Bentley-Condit and Smith 2010). Moreover, tool use behaviour can be observed even in phylogenetically distant species. For instance, species of insects and apes use sponge-tools to collect and transport liquid food; Lőrinczi (2014) has reported that ants (*Aphaenogaster subterranea*) use small objects (e.g., bits of pine needle, cone, and bark) as tools to collect and transport liquid food to their nest in the wild. Additionally, in an experimental setting, two species of funnel ants (*Aphaenogaster subterranea* and *Aphaenogaster senilis*) were able to select tools with a good soaking capacity, even if the tools were artificial materials that could not be found in their natural environment (Lőrinczi et al. 2018; Maák et al. 2017). In apes, it was shown that wild chimpanzees (*Pan troglodytes schweinfurthii*) in the Budongo Forest Reserve, in Western Uganda, manufacture sponges from leaves or mosses to extract various types of liquids from cavities and rivers (Lamon et al. 2018); they dip the sponge into the liquid, allow it to soak up the liquid, and squeeze it in their mouth. Furthermore, chimpanzees that were exposed to a novel situation (the location and liquid type in the novel task were unrelated to the original ecological context of moss-sponging) preferred moss-sponges—which have a better soaking capacity—to leaf-sponges, which have an inferior soaking capacity (Lamon et al. 2018).

Definition of tool use

Over the last 30 years, the most widely used definition of tool use is the one suggested by Beck (Hunt et al. 2013). Beck (1980, p. 10) defined tool use as follows:

> The external employment of an unattached environmental object to alter more efficiently the form, position, or condition of another object, another organism, or the user itself when user holds or carries the tool during or just prior to use and is responsible for the proper and effective orientation of the tool.

In both aforementioned cases of chimpanzees and ants, the animals employ the unattached environment objects (i.e., sponge-tools) to alter the position of another object (i.e., liquid) from the ground (in the case of ants) or cavities (chimpanzees) to their nest or mouth; thus, both behaviours

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were consistent with the definition set forth by Beck. Thirty years later, Shumaker et al. (2011) updated the definition by Beck (1980), including a manipulable attached environmental object as a tool; according to Beck's original definition, for example, if the sponge tool is tied to the ground by a long string, it cannot be regarded as a tool owing to its attachment to the ground. According to the updated definition (Shumaker et al. 2011), the sponge can be regarded as a tool because it is manipulable.

Moreover, St. Amant and Horton (2008, p. 1203) proposed the following modified definition:

> Tool use is the exertion of control over a freely manipulable external object (the tool) with the goal of (1) altering the physical properties of another object, substance, surface of medium (the target, which may be the tool user or another organism) via a dynamic mechanical interaction, or (2) mediating the flow of information or other organisms in the environment.

Thus, and like Shumaker et al. (2011), St. Amant and Horton (2008) regarded manipulable attached objects as tools, but the latter also added breadth to the tool use definition; they considered that objects not used to alter the form, position, or condition of another object could be regarded as tools. For instance, a study showed that a wild gorilla (*Gorilla gorilla*) used a stick to test the depth of the water when it was wading through (Breuer et al. 2005); based on St. Amant and Horton (2008)'s definition, this denotes tool use because it was used to mediate the flow of information in the environment. However, Crain et al. (2013) asserted that the definition of tool use needs to be updated owing to the continuous report of tool use behaviour based on variables that are not encompassed by these prior definitions (Bentley-Condit and Smith 2010).

Still, even if a behaviour conforms to the definitions, it cannot be concluded that the tool user understands the physical relationships between the tool and the other object; instead, it is possible that animals display such complex tool use behaviour through innate disposition, stimulus generalization (i.e., the transfer of a learned response from one stimulus to another similar stimulus; Mazur, 2016), or trial-and-error learning (i.e., learning from the consequences that followed certain reactions of the animal; Snoddy, 1920). In comparative cognition research especially, the cognitive aspects underlying tool use behaviour are important; thus, in the next section, I introduce complex tool use behaviours that were observed in wild primate and avian species and recent studies that have tested experimentally, whether animal tool use occurs based on their understanding of the physical causal relationships between their actions and the results of these actions (hereinafter tool functionality).

Cognition underlying complex tool use behaviour in animals

Some previous studies have reported that wild animals, mainly primate and avian species, can skillfully use tools (Bentley-Condit and Smith 2010). For instance, for primates in a wild setting, researchers observed that New World capuchin monkeys (*Sapajus libidinosus*) and chimpanzees (*Pan troglodytes verus*) were able to place hard-shelled palm nuts on anvils (e.g., boulders and logs) and use hammer stones to crack the nuts open (Visalberghi et al. 2015). In avian species, wild New Caledonian Crows (NC crows; *Corvus moneduloides*) were shown to be able to manufacture hook-tools from a pandanus leaf and manipulate them with their bills to extract larvae from holes in living and dead wood (Hunt 1996).

Now, these findings beg the following question: do these animals demonstrate such skillful tool use while understanding tool functionality? In comparative cognition research, some scientists have attempted to examine the cognitive aspects underlying such tool use through the following methods: experimental observational method (a method of observation in which some kind of experimental manipulation is added to the animals' living spaces) and experimental analysis method.

Hammer tools in nonhuman primates

Reportedly, the nut-cracking behaviour (mainly observed in capuchin monkeys and chimpanzees) was the most complicated form of tool use among nonhuman animals, as it requires complex movement (i.e., asymmetrical bimanual movement and finger-precision grips) and the optimal choice of stones as tools (Foucart et al. 2005). One prior study reported that capuchin monkeys do not choose stones for nut-cracking at random but, instead, select more effective stones for cracking the nuts, namely, stones that are heavy and sturdy enough to overcome the resistance of the nutshell (Visalberghi et al. 2009). Specifically, this study went on to present pairs of natural or artificial stones to wild capuchin monkeys; each pair comprised two stones of different sizes, weights, or friability, and there was a contradiction between the size and weight in the pairs of artificial stones. Namely, the monkeys could not predict the weight of the artificial stones from the size because, while the functional stone was small and heavy, the nonfunctional one was light and large. Summarizing, the monkeys ultimately chose the functional stone, transported it to the anvil, and used it; in the artificial stones condition, they gained information about the weight of the stone by moving, lifting, and tapping them. Similarly, wild chimpanzees were observed to employ this flexibility while choosing stones as tools (Sirianni et al. 2018).

However, some studies demonstrated that capuchin monkeys were not able to completely understand the physical causal relationships in tool use situations. For example, in a recent study (Painter et al. 2019), captive capuchin monkeys were required to choose one of two tools based on the spatial arrangements of a hook-shaped tool and a food reward. They could obtain the reward just by pulling one of the tools, but they could not obtain it by pulling the other tool. Painter et al. (2019) reported that the monkeys failed to attend to the functional spatial relationship between a tool and a reward in a tool-choice task.

Tool manufacture in avian species

In the wild, very few animal species habitually manufacture tools for foraging (Shumaker et al. 2011). NC crows are known to be the most proficient tool manufacturers (Knaebe et al. 2017); still, a recent report showed that captive Hawaiian crows (*Corvus hawaiiensis*) spontaneously manufactured tools without training (Klump et al. 2018).

Some researchers have investigated, in experimental settings, the extent to which NC crows and Goffin's cockatoos (*Cacatua goffiniana*) could manufacture stick tools in different situations and if they could be flexible regarding the manufacturing under different circumstances (Auersperg et al. 2018; Knaebe et al. 2017). Specifically, crows were required to manufacture a stick tool by cutting the stick from tree branches with their beak, to insert the tools in the opening of a transparent apparatus, and then extract a food reward placed inside the apparatus (Knaebe et al. 2017); the results showed that the crows were able to manufacture relatively shorter tools when the distance between them and the reward was relatively short, and relatively longer tools when the distance was relatively long. They showed such flexibility when manufacturing even when they were not able to see the branches and the apparatus simultaneously because of a visual barrier. However, they showed low success rates for the extraction of the reward. Knaebe et al. (2017) concluded that NC crows have a degree of flexibility, but the degree is not clear.

The study on Goffin's cockatoos, which are not habitual tool users, showed that they were able to manufacture stick tools from cardboard while adjusting the length of the tools by the distance between the opening of the apparatus and a food reward (Auersperg et al. 2018); the tasks were similar to those conducted in NC crows (Knaebe et al. 2017). However, the cockatoos could not adjust the widths of the tools relative to the opening of the apparatus; thus, future studies are warranted to reveal how animals recognize the relationships between multiple objects in the world and their ability to understand the physical causal relationships behind the tool use situations. Tool use behaviours in nonhuman animals may become *tools* to elucidate the neural mechanisms of tool use disorders in humans.

Application of tool use tasks to physiological psychology: tool use as a method to establish an animal model of ideational apraxia

Tool use disorder in humans

In a case study (Ochipa et al. 1989), a human patient was presented with a toothbrush, a comb, and eating utensils (including a spoon) that were located at the side of a dinner tray; this patient ate with the toothbrush and brushed his teeth with the spoon and comb. Moreover, although he was capable of naming and pointing to the tools when they were individually named by an examiner, he was not capable of pointing to the tools when they were described by function; this was a case of a 67-year-old patient with ideational apraxia, which is characterized by tool use disorder.

Ideational apraxia is a subtype of apraxia, and apraxia is defined as the inability to perform skilled or learned movements in the absence of elementary motor, sensory, or coordination deficits that could serve as the primary cause of apraxia (Park 2017). Meanwhile, ideational apraxia is characterized by the inability to conceptualize tool use tasks despite intact identification of the tools (Park 2017); this apraxia subtype is mainly caused by diffuse brain lesions and dementia (Goldenberg 2003). As aforementioned, patients with ideational apraxia cannot, for example, choose a spoon to eat soup when choosing among a set of tools in a kitchen cupboard.

Recently, many studies have attempted to reveal the neural mechanisms underlying tool use behaviour in humans; they did so by examining patients with brain damage who undertake tool use tasks (Goldenberg and Spatt 2009; Osiurak et al. 2018). In these studies, participants were asked to select a tool among various tools with different shapes or rigidities and use it to obtain a target. The tools were novel for participants, and they could obtain the target only by understanding tool functionality, and selecting suitable tools based on the shape or spatial arrangements of the target and an obstacle in the apparatus—which was placed between the target and participants. The range of the brain damage was analyzed using neuroimaging techniques, including magnetic resonance imaging and computed tomography. By using this approach, researchers investigated which brain areas contributed to the understanding of tool functionality in novel situations by testing the relationships between lesioned brain areas and participants' performance (i.e., number of selections of the correct or erroneous tools) in the tool use tasks. If patients with lesions in a specific area could not select the tools correctly, the area was considered to contribute to the understanding of tool functionality in novel situations. These studies suggested that the left inferior parietal cortex (Osiurak et al. 2018), and the middle frontal, precentral, supramarginal, inferior parietal, and superior parietal cortices (Goldenberg and Spatt 2009) contribute to this understanding.

In clinical studies, however, a more in-depth identification of a brain area that contributes to how the individual understands tool use is difficult because there are large individual differences in the range of brain damages. Thus, animal models of ideational apraxia could be useful to reveal the neural mechanisms that support flexible tool use behaviour and to develop methods for rehabilitation of tool use disorder. Specifically, tool use tasks conducted mainly using comparative cognition approaches would be useful to evaluate animals' behaviours with a specific lesioned brain area.

Which animal species would be suitable to be used?

To the best of my knowledge, there are no animal models of apraxia. Recent studies have investigated the neural mechanisms of tool use, focusing on macaque monkeys (Bretas et al. 2020). For example, a study on Japanese monkeys (*Macaca fuscata*) suggests that the intraparietal region, basal ganglia, presupplementary motor area, premotor cortex, and cerebellum contribute to tool use behaviour

(Obayashi et al. 2001). Specifically, using positron emission tomography, Obayashi et al. (2001) showed that tool-use-related activities significantly increased cerebral blood flow in these areas.

However, using rodents could facilitate more intensive study of the neural mechanisms underlying tool use. This owes to factors such as: (1) we currently have greater knowledge of the anatomical and molecular biological features of the brain of rodents than those of nonhuman primates; (2) studies using rodents would enable researchers to employ various manipulations (e.g., microinjections of drugs into specific areas and electrocautery lesions made in specific areas) that cannot be employed in humans and nonhuman primates (Cenci et al. 2002); and (3) the cost of caring for rodents is relatively low (Kirse et al. 1996).

In rodents, a study used degus (*Octodon degus*) to investigate the neural mechanisms of tool use (Kumazawa-Manita et al. 2013) and found that tool use learning augmented adult neurogenesis (i.e., birth of new nerve cells) in the hippocampus. I followed up on this work and chose to use rats (*Rattus norvegicus*) as subjects because they are more available as experimental animals for potential future studies in many research fields.

In behavioural studies, it is common to use a variety of laboratory rat strains, such as non-pigmented (e.g., Wistar), partially pigmented (e.g., Long-Evans), and fully pigmented (e.g., Brown-Norway) (Prusky et al. 2002). In tool use tasks, subjects are required to visually observe tools and targets and appropriately manipulate the tools; it has been shown that Norway rats have better visual acuity than other strains (Prusky et al. 2002). Thus, I used Brown-Norway rats in four studies (Nagano 2019a, 2019b, 2021; Nagano and Aoyama 2017a) and both Brown-Norway and Long-Evans rats in one study (Nagano and Aoyama 2017b).

Which tool use tasks are most appropriate for rats?

To show the effect of a specific brain lesion on tool functionality understanding in tool use tasks, first, researchers need to demonstrate that animals without any brain lesions can understand physical causal relationships in the tasks. That is because, if the performance of an animal species in the task is too low even in individuals without any brain lesions, it cannot be concluded that their low performance after surgery was caused by the lesion in the specific brain area owing to a floor effect.

Regarding rodents, two previous studies found that degus could use a rake-shaped tool to retrieve food rewards that were beyond their reach after undergoing step-by-step trainings (Kumazawa-Manita et al. 2013; Okanoya et al. 2008). Specifically, the training procedure in both studies was a modified version of the procedure developed for Japanese macaques, and the distance between the rake and the reward was made increasingly longer (Kumazawa-Manita et al. 2013; Okanoya et al. 2008). The degus were able to obtain the reward even when it was placed on the side of the rake, requiring the manipulation of the rake laterally to reach the reward before pulling the rake.

Moreover, in the transfer tests (Okanoya et al. 2008), the degus were tasked with choosing either a functional or a nonfunctional rake-shaped tool to obtain the reward; the functional rake had been the one used in the trainings, whereas the nonfunctional rake (i.e., the blade was raised by wires, so the blade went over the reward when it was pulled) was used only in the tests. The degus were able to choose the functional over the nonfunctional rake, suggesting that they showed functional understanding of the tool. However, the degus may have chosen the functional rake simply because it was used in the training (i.e., simple stimulus generalization); namely, this study is not conclusive on whether these rodents can understand tool functionality.

Studies have remarked on the necessity of conducting tool use task studies in which rats can obtain rewards by simple actions that require no physical dexterity, mainly because they are a non-tool-using species in the wild (Bentley-Condit and Smith 2010). In our study (Nagano and Aoyama 2017a), we used the tool-choice task experiment, and the procedures were like those used in studies on nonhuman primates (e.g., Hauser 1997; Painter et al. 2019) and birds (Tebbich et al. 2010). In the trainings, subjects were required to choose one of two hook-shaped tools to obtain a reward (Figure 19.1).

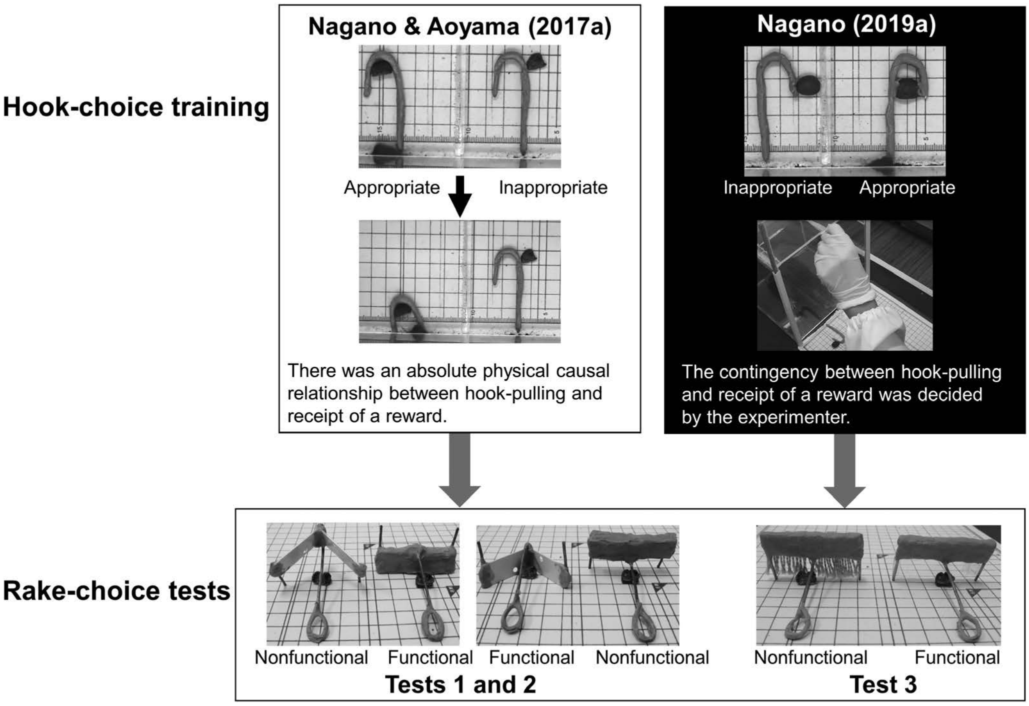

Figure 19.1 Outline of the tool-use tasks in our studies. This figure is a modified version of the one published in Nagano (2019a), and the owner of the copyright of the published figure is the author of this chapter

The two hook options differed regarding the spatial arrangement of the hook and the reward. If subjects chose the appropriate hook, they could obtain the reward because the reward was placed inside the hook. By contrast, if they chose the inappropriate hook, they would fail to obtain the reward because the reward was placed outside the hook. The two hooks and two rewards were placed in these arrangements before each trial start, and subjects could obtain the reward by perpendicularly pulling the appropriate hook to themselves. In such procedures, the relationship of the tool and the reward, defined as an action on one object (e.g., appropriately arranged hook) that affects a second object (e.g., food reward) occurs by default; thus, it is categorized as a zero-order relation, and some researchers do not regard actions involving a zero-order relation as tool use (Visalberghi and Fragaszy 2012). In our studies, we did not place importance on whether task-related observed behaviours conformed to the definition of tool use, and we used tasks called "tool use tasks" as a useful measure to test their tool functionality understanding. Both in complex tool use (i.e., nut-cracking and tool manufacturing) and in the simple tool-pulling tasks, it is important to detect subjects' understanding of physical causal relationships between multiple objects.

In most of our studies, rats were required to use tools to obtain foods that were beyond their reach (Figure 19.2). However, one of the most frequently used behavioural tasks in studies with rat subjects is the lever-pressing task in an operant chamber (Konorski and Miller 1937). Rats can learn to press a lever to obtain a pellet if the lever is electrically connected to a feeder filled with food pellets. What are the differences between tool use and lever-pressing behaviour? Rats can learn that there is a pellet in a food cup and that they will have access to this pellet after they press a lever (i.e., a mechanism of two events) only after they repeatedly experience the presentation of a pellet following their lever-pressing; thus, such experiments do not allow for interpretations regarding whether rats in an operant chamber can understand *why* a pellet is present in a food cup after they press the lever. Contrastingly,

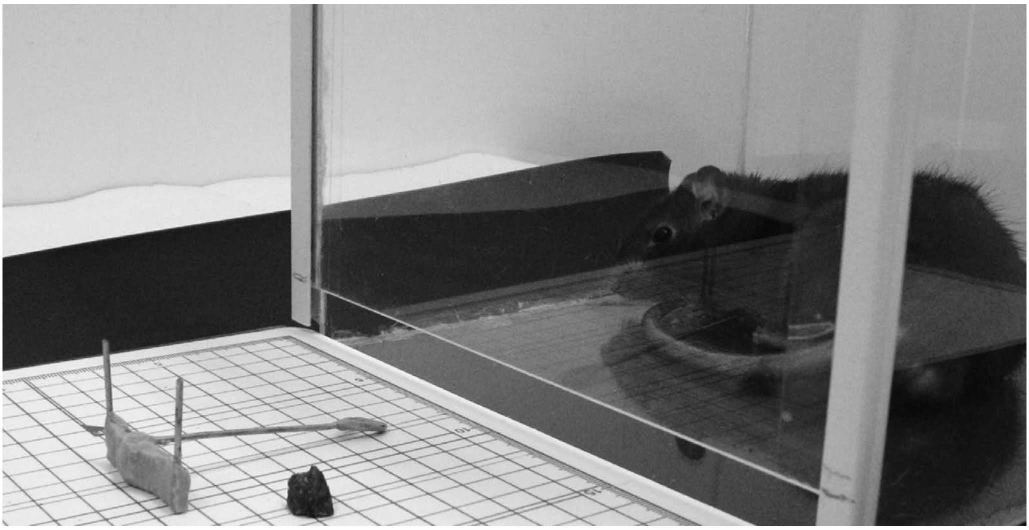

Figure 19.2 An example of a tool use task. The rats could manipulate tools to obtain food rewards through the space between the sliding door of the experimental box and the experimental board

in tool use tasks (e.g., hook-choice), it is possible for rats to understand physical relationships between the pulling of the tool and the approaching/pulling of the food reward (i.e., a mechanism of two events) before they take action; if rats can understand the relationships, they supposedly can solve tasks, even when exposed to completely novel situations.

Tool-choice in normal rats

In this section, I describe studies about tool-choice in rats without any brain lesions (Nagano and Aoyama 2017a). Eight experimentally naïve Brown-Norway rats received hook-choice training to be able to choose appropriately arranged hooks; this was done because naïve rats do not spontaneously pull tools in experimental settings. Thus, they had to be trained to pull the hook to obtain a food reward; we did so by using a procedure in which the reward was placed inside the hook and the distance between the combination of the three parties (i.e., the hook, the reward, and the rat) was made increasingly longer during hook-pulling training. This training was done before the hook-choice training. In the hook-choice training, we used 12 arrangements of hooks and rewards, with each daily session comprising 36 trials; all rats chose appropriate hooks in 30 or more trials in two consecutive sessions from 15–41 sessions.

After the training, we conducted three rake-choice tests. In the tests, we investigated whether rats could choose functional tools even when exposed to novel tools, without additional training. Each test was conducted only for a session (36 trials); to deny the possibility that the rats would choose the functional tools by simple stimulus generalization (i.e., from the training to the tests; Figure 19.1), the rake-shaped tools that were used in the test differed from those in the hook-choice and hook-pulling trainings regarding shape, color, or texture. Each test used a functional and a nonfunctional rake; if the rat pulled the functional rake perpendicularly, it would obtain the reward. Each functional rake that was used in Tests 1 and 2 could be turned into a nonfunctional rake by placing it upside down so that there was empty space under the blade; accordingly, if the rat pulled a nonfunctional rake, it would not obtain the reward because the rake would not pull the reward. Instead, the blade of the rake would just pass over it.

In Test 1, one rake was the functional and the other, nonfunctional; we reversed this combination in Test 2. In both tests, all rats were capable of choosing functional over nonfunctional rakes.

Thus, rats may have chosen the tools depending on the contact between the blade of the rakes and the horizontal surface (i.e., if in contact, functional; if not, nonfunctional), thus differing from the hook-choice training. In Test 3, the appearance and the functionality of the two rakes were contradictory (Figure 19.1); the functional rake had a hard and transparent acrylic plate under the blade, and the nonfunctional rake had soft and opaque embroidery threads under the blade. In Test 3, no rat could choose the functional over the nonfunctional rake. Thus, rats seem to have a basic ability to understand physical relationships when there is no contradiction between tool appearance and functionality.

Experimental control in the tool-choice task for testing the effect of a specific brain lesion on tool use, and a methodological suggestion

Even if subjects with a specific brain lesion were to not choose functional rakes in the aforementioned Tests 1 and 2, this would not be enough to prove that the lesions impaired their tool functionality understanding in novel situations; it would be possible that lesions impair their fundamental abilities (i.e., visual, motor, or spatial perception), not their tool functionality understanding. To prove this, we need control tasks very similar to tool use tasks and that exclude tool-use-specific factors.

Studies on Japanese monkeys (Obayashi et al. 2001) and degus (Kumazawa-Manita et al. 2013) reported that tool use behaviour induced a significant increase in cerebral blood flow in specific areas or adult neurogenesis in the dental gyrus of the hippocampus, whereas control tasks did not induce any neural changes. In both studies, subjects manipulated a rake to obtain food that was placed beyond their reach. In primates, the control task was a simple stick-manipulating task whereby monkeys were rewarded if they swung a simple stick fixed to a plate with a universal joint (Obayashi et al. 2001). In rodents, it was a spatial learning task in a radial arm maze (Kumazawa-Manita et al. 2013). However, there were non-tool-use-specific differences (e.g., the differences related to the simple movement required to obtain rewards).

In my study (Nagano 2019a), therefore, I aimed to develop a control task for the tool use task, the hook-choice training (Nagano and Aoyama 2017a). There were no tool-use-specific factors in the control training (Nagano 2019a), namely, there was no absolute physical causal relationship between the manipulation of objects with a similar appearance and the food approaching the subject (Nagano and Aoyama 2017a). The experimenter manipulated the contingency (i.e., the relationship of the antecedent stimuli/behaviour and the consequences of the behaviour) between these two events. Specifically, fake foods were used for both appropriate and inappropriate hooks (Figure 19.1); when the fake food entered the box by the pulling of the appropriate hook, the real food reward was inserted by the experimenter in a small hole in the door of the experimental box immediately after. For the inappropriate options, the fake food was fixed to the surface of the experimental board with double-sided tape. Accordingly, there were no significant differences in the number of sessions until each rat attained the criterion between the two studies, except for one rat (Nagano 2019a). In the rake-choice tests, which were equal to those in Nagano and Aoyama (2017a), no rats chose the functional over the nonfunctional rakes in both Tests 1 and 2. Although one rat chose the functional rake significantly more than the nonfunctional rake in Test 3, it did not choose the functional rakes in Tests 1 and 2.

Thus, I suggest the tool use tasks methodology in our studies (Nagano 2019a; Nagano and Aoyama 2017a) for future research aimed at revealing specific brain areas contributing to tool functionality understanding in novel situations (Table 19.1). Specifically, all rats could be trained to pull a hook to obtain a reward; between the hook-pulling and hook-choice training, half the rats could have a specific brain area lesioned (lesion group). To this end, a part of their skull will be removed, and a neurotoxin will be injected using a microinjector at multiple positions of the specific area based on the stereotaxic coordinates (Roberts 2013). To exclude the possibility that behavioural changes in the lesion group are owed not to the lesion but to the surgery, in the remaining half (sham lesion group: control group), we will also insert the needle of a microinjector—including either no solution or an

Table 19.1 Prediction of the results of each group in each training and test when a specific brain area which contributes to physical causal understanding is lesioned

Index of performance	*Hook-choice training*		*Rake-choice tests post-lesion*	
	Pre-lesion	*Post-lesion*	*Tests 1 and 2*	*Test 3*
	Number of days required to attain the criterion		*Choice rate of the functional rake (Above the chance level?)*	
Nagano and Aoyama (2017a)	Lesion = Sham lesion	Lesion > Sham lesion	Lesion: No Sham lesion: Yes	Lesion: No Sham lesion: No
Nagano (2019a)	Lesion = Sham lesion	Lesion = Sham lesion	Lesion: No Sham lesion: No	Lesion: No Sham lesion: No

The hook-choice training in Nagano (2019a) excluded tool-use-specific factors. The rake-choice test procedures were equal in both studies.

artificial cerebrospinal fluid—to the same area as the lesion group. After the recovery period following surgery, the hook-choice training and rake-choice tests could be conducted based on either of the following studies: Nagano (2019a) or Nagano and Aoyama (2017a). The number of days required to attain the criterion in the hook-choice training and in the choice rate of the functional rake could be useful measures of performance. Subsequently, if this methodology provides results for a lesion group that has a performance worse than that of the control group in the hook-choice training (i.e., including tool-use-specific factors) and in tests 1 and 2, and there are no between-group differences in the other training sessions/tests, we may be able to conclude that the lesioned area contributes to tool functionality understanding in a tool use situation. That type of finding would indicate that such lesioned rats could be good candidates for animal models of ideational apraxia.

Future tool use work among animals

Several tool use-related studies conducted among various animal species could contribute toward elucidating the evolutional mechanisms underlying physical causal understanding and the cognitive mechanisms of this understanding. For instance, it would be valuable to investigate the effects of sociality on this understanding. Among rodents, data concerning tool use has been overwhelmingly lacking. Rodents have many different types of social structures (Gromov 2017). For example, degus and naked mole rats (*Heterophalus glaber*) have highly social community structures (Gromov 2017). In contrast, California ground squirrels (*Spermophilus beecheyi*) are usually solitary (Coss and Owings 1978). Captive naked mole rats spontaneously use tools (Shuster and Sherman 1998), and degus can become accustomed to using tools through training (Kumazawa-Manita et al. 2013; Okanoya et al. 2008). Furthermore, wild California ground squirrels use sand as a tool for attacking snakes (Owings and Coss 1977). However, the physical causal understanding of each species through the use of common behavioural tasks has never been investigated. Future studies using common tool use tasks can investigate how social structure-related differences can influence their understanding and reveal which sociality factors among humans promote their understandings of physical relationships between multiple objects.

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20

BRIDGING THE GAP BETWEEN HUMAN LANGUAGE AND ANIMAL VOCAL COMMUNICATION

Sabrina Engesser and Simon William Townsend

Human language

Language is a hallmark that defines humans, and one that distinguishes us from other non-human animals ("animals" hereafter). Language enables the exchange of information in open-ended ways, and the communication of concepts only limited by the human mind (Hockett 1960). This language faculty builds on core abilities that were long thought to be uniquely human, but where recent advances in the field of animal communication demonstrate intriguing human-animal parallels. This chapter is devoted to discussing some of the most intriguing findings of recent years, where studies on animal communication can offer a glimpse into understanding the evolution of human language. In doing so, we will focus on two cornerstones of the language faculty: the ability to intentionally communicate information through learned signal-meaning mappings (*semanticity*), and on combinatorial mechanisms where sounds and signals are combined to communicate more diverse messages (*combinatoriality*).

Semanticity and combinatoriality in human language

At the most basic level, language's capacity rests on the ability to communicate semantic information, that is, to represent concepts symbolically (Hockett 1960). In particular, this ability allows us to assign arbitrary acoustic labels, or "words", to any internal or external concepts, whose comprehension and production we learn via input from the surrounding communicative environment (e.g., we learn that feathered animals are called "birds"). This ultimately requires speakers to understand and converge on the meaning and structure of the used words and involves a representation of the words' meaning in the communication partners' brains, linking acoustic structures with concepts. But not only can we assign acoustic labels or words to any concepts, we also communicate those intentionally to voluntarily and purposefully share and exchange information.

Whilst the ability to communicate semantic information is clearly one of the most fundamental cornerstones of human language, it is our combinatorial capacity that further amplifies our communicative output. Specifically, human language is generative in such a way that we can communicate limitless, more diverse, meaningful expressions by making use of a limited set of acoustic units or symbolic labels (Hockett 1960). At the phonological level, meaningless sounds or building blocks can be combined in different arrangements to create large repertoires of meaningful words. For example, the sounds, or "phonemes", /a/, /t/, /k/, and /h/ are themselves meaningless but can be reused and combined in different ways to generate the meaningful words "at", "cat" or "hat". At the higher

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compositional layer, such meaningful words can then be assembled to create higher-order phrases to communicate derived, more diverse and complex expressions. For example, "cat" and "hat" can be assembled with other words to create the phrase "cat in the hat".

Together, human language's semantic and combinatorial capacity enables us to communicate any concepts, irrespective of their novelty, in a productive and open-ended way, constituting language's generative nature. Understanding how such vocal complexity arose represents a contentious debate, and one way to investigate this is through searching for analogues in the communication system of other animals. Specifically, such parallels can provide insights into early precursorial forms of human semantic and combinatorial abilities, and shed light on convergent factors that drove their emergence in human and animal communication systems.

Analogues in animal vocal communication?

Evidence from various species suggests that analogue forms of semantic and combinatorial abilities also exist in the communication systems of other animals. In particular, work on primate species has revealed promising insights demonstrating similarities in the way animals communicate and derive meaning and engage in information sharing (Townsend et al. 2020). While such studies suggest parallels in the emergence of symbolic communication, whether such data on animals can be considered as comparative examples to human language's semantic communication is, however, contentious. We will address this in the first half of the remaining chapter and will discuss the extent to which such critiques might be inaccurate and outdated. In the second half of the chapter, we will then present analogues to language's combinatoriality. We will show that there exist considerable similarities regarding the ways in which animals can combine acoustic units into larger arrangements and sequences to communicate information; some of which appear to resemble language's phonology and compositionality, with others representing more intermediary forms (Engesser and Townsend 2019).

Semanticity in animal vocal communication?

The meaning of animal vocalisations represents one of the most conceptually and empirically productive areas of animal communication (Townsend and Manser 2013). However, given the, at times, unavoidable tendency to comment on the evolution of semantics in language, such research has simultaneously been plagued by controversy (Owren et al. 2010). A core point of contention is that animal vocalisations and human words are assumed to be non-comparable semantically (Rendall et al. 2009). Although there are a number of superficial similarities – both serve a communicative function, both transfer information etc., extrapolating further to reach beyond this is neither helpful or relevant – a misguided endeavour providing little evolutionary insight. In this section, we review some of the key criticisms levied against research on "meaning" in animal communication and its link to linguistic semantics, and highlight how existing data holds promise in bridging this gap between language and animal communication systems.

Functional referentiality in animal calls

The first research to link animal vocalisations and human words came out of the lab of Peter Marler in the 1980s. Specifically, Dorothy Cheney and Robert Seyfarth showed that vervet monkeys (*Chlorocebus pygerythrus*) produced acoustically distinct alarm calls to different threats: aerial and terrestrial. Given the probabilistic relationship between the external threat and the acoustic structure of the vocalisation, Seyfarth et al. (1980) argued vervet alarm calls may refer to objects or events just as human words, such as "eagle" or "leopard", symbolise different predator types. Furthermore, they devised an inspired experiment demonstrating these calls are also meaningful to receivers. If alarm calls encode presence of a putative threat, then when playing these calls back in the absence of any threats, receivers should respond *as if* they have encountered such a predator – running into trees after terrestrial alarm calls and looking into the sky after hearing aerial alarm calls. This is indeed what Seyfarth et al. observed, strengthening the claim that these calls hold some semantic value that is processed by receivers. Since the ancestral system from which language evolved would have been more primate than human like, these data have been suggested to shed light on precursorial forms of semantics which could have then served as the evolutionary "feedstock" giving rise to our own semantic abilities. Are monkey alarm calls therefore precursors to human words?

A decade later, and again under the supervision of Peter Marler, Chris and Linda Evans addressed the semanticity question in chickens (*Gallus gallus*). Like vervet monkeys, chickens produce acoustically distinct vocalisations when encountering external predators (Evans et al. 1993). Additionally, playback experiments revealed that these calls are meaningful to receivers, since individuals engaged in relevant antipredator behaviour upon exposure even when predators were not present (Evans et al. 1993). If vervet monkey vocalisations were semantic then, by extension, so were chicken alarm calls. However, perhaps given the phylogenetic distance between humans and chickens, rather than couching chicken vocalisations in linguistic terminology, Evans and colleagues took a more pragmatic approach and focused on the call's function rather than its' "symbolic meaning": chicken alarm calls functioned *as if* they referred to external events (Evans et al. 1993; Macedonia and Evans 1993). The motivation for this more conservative analysis was due to ambiguities in the proximate cognitive mechanisms underlying animal vocal communication. Linguistic semantics necessarily involves a suite of production and perception-based mechanisms that, at the time, could not be investigated in animals. Hence any similarities between context-specific calls in animals and human words were surface-level, ultimately complicating any discussion of precursor forms (in primates) or, in the case of chickens, evolutionary convergence. This issue has continued to plague the field of animal referential communication and the evolution of semantics. But what if we could investigate these mechanisms? What if we can begin to bridge the apparent chasm separating animal vocalisations and human words? As will be demonstrated in the following sections, researchers have already done this, yet these findings continue to escape discussion of the evolution of semantics.

Mental representation of call meaning

One of the major hurdles precluding comparison involves the issue of mental representation. In language, word meaning is decoded through engaging a mental representation that is associated with a particular stimulus category (Evans and Evans 2007). Therefore, if animal calls really *stand for* something in the environment, call processing should be representationally based. Zuberbühler et al. (1999) addressed this question in Diana monkey (*Cercopithecus diana*) alarm calls. In an elegant experiment, Zuberbühler et al. showed that monkeys initially presented (or "primed") with eagle shrieks (calls produced by the predator itself) responded weakly to subsequent eagle alarm calls (monkey calls referencing predator type). Conversely, when primed with leopard growls and then exposed to (or "probed" with) an eagle alarm call, monkeys responded with classic anti-aerial-predator behaviour. What explains this? In both instances the prime and the probe stimulus were distinct, ruling out the possibility that responses to alarm calls are reflexive motor responses driven solely by the differing acoustics of the call (i.e., "perceptual processing", Zuberbühler et al. 1999). Instead, what better explains the differences in behaviour was the vocalisation's putative referent. In the eagle shriek – eagle alarm call condition, the referent was identical, both eagle shrieks and eagle alarm calls are associated with eagles. In the leopard growl – eagle alarm condition the referent is different. Parsing of alarm calls in Diana monkeys therefore seems to be conceptually, rather than perceptually, driven – in other words when monkeys hear alarm calls this actively engages a representation of a specific predator, aerial or terrestrial.

A few years later, almost identical findings were found for domestic chickens. Evans and Evans (2007) showed that food calls evoke retrieval of information regarding food discovery. When hearing food calls, chickens were more likely to engage in food-searching behaviour – a response that was dampened when chickens were exposed to or "primed" to the presence of food prior to hearing food calls. This phenomenon has been most recently tested in Japanese tits (*Parus minor*). Through manipulating the experience of subjects (i.e., what they saw) when hearing referential alarm calls, Suzuki (2018) demonstrated that birds became more visually perceptive to objects resembling snakes when hearing snake alarm calls. It may well be that even prior to seeing a predator, Japanese tits mentally retrieve a snake-specific visual image or representation upon hearing snake alarm calls. These behavioural findings have received support from neurophysiological work. Gifford et al. (2005) showed that in rhesus macaques (*Macaca mulatta*), acoustically distinct harmonic arches and warbles – both of which refer to the presence of high-quality food – activated the same brain region, namely the ventral prefrontal cortex (vPFC). Not only does this suggest that rhesus macaques classify calls based on their conceptual rather than perceptual (acoustic) similarities/features, but that this is processed in an analogous brain area important in semantic content processing in humans (Gifford et al. 2005). Minimally, what these results indicate is that in functionally referential animal communication systems in which the representation of the signal has been investigated, there are striking behavioural and neuro-physiological parallels with word processing in language.

Intentional communication of meaning

Together these data arguably provide one plank of the metaphorical bridge between animal vocalisations and human words. If animals label external events with acoustically distinct calls and represent these calls in executive parts of the brain (areas of the brain where more sophisticated processing occurs), perhaps they can genuinely help us understand the evolutionary progression of semantics in the broad sense. Granted, receivers are capable of integrating and processing information conveyed by calls in intriguing ways (Arnold and Bar-On 2020), however in language, communication is driven by the underlying intention to communicate which is itself dependent on an understanding of the meaning with which words are imbued (Rendall and Owren 2013). In short: human signallers and receivers converge in how they represent words. Until recently, the overwhelming consensus, at least in comparative psychology, has been that animal signallers are blissfully unaware of the communicative value of their signals and pay little-to-no regard to what receivers know when communicating (Tomasello 2010). Recent observational and experimental developments however suggest this picture is inaccurate. An impressive body of data suggests that animals are sensitive to the presence of potential receivers and modify their calling behaviour in dynamic ways to account for this. Playbacks in chimpanzees (*Pan troglodytes*) simulating the presence of group members have further experimentally confirmed that vocalisations are not indiscriminately broadcast but directed at individuals, in this case, 'friends' (Schel et al. 2013a). Furthermore, snake presentation experiments, again in chimpanzees, have shown that alarm call deployment is both goal-directed and fulfils key criteria devised to demonstrate intentional communication: response waiting, gaze alternation and signal elaboration (see Schel et al. 2013b). Similar experiments have also probed the knowledge-state of receivers and its influence on calling, providing tantalising evidence that chimpanzee signalling behaviour may involve attributing mental states to others (i.e., ignorant vs. knowledgeable, Crockford et al. 2012). Given the accumulating data, it would therefore seem reasonable to re-evaluate the assumed dichotomy between oblivious signallers and representing receivers (i.e., engaging mental representations when processing signals) and entertain the idea that signals are potentially mentally represented in both communicative parties. Is this therefore another step towards evidence of animal communication patterns analogous to human semantic communication?

The role of learning

Not only are words represented in signallers' and receivers' minds, but they are also acquired from the input (Cameron-Faulkner et al. 2003). Raise a child born in the UK in Tanzania and they will speak Swahili. Simply put, words need to be learned. Animal referential calls, however, are often considered to be innate, tightly coupled to the underlying arousal state experienced by the signaller, and closed to vocal learning processes (Wheeler and Fischer 2012). This does not mean deployment or usage is not moulded by experience (see Seyfarth and Cheney 2010), but rather the fine articulation to accurately imitate a vocal stimulus is highly constrained. If accurate, this would represent a key discontinuity with words and arguably call into question any endeavour to try and bridge the gap between human semantics and animal calls. However, recent data on chimpanzee food calls have cast doubt on the generality of this assumption, but not without controversy.

Upon encountering food, chimpanzees produce acoustically distinct vocalisations that vary reliably with food quality (Slocombe and Zuberbühler 2005, 2006). Furthermore, playback experiments confirm that these calls convey information on the presence of high or low quality food to receivers (Slocombe and Zuberbühler 2005). Given the call's production/perception specificity they clearly fulfil the predefined criteria set out to identify a call as functionally referential (Macedonia and Evans 1993). Follow-up observational and experimental work in the wild has also demonstrated chimpanzees deploy these calls voluntarily and direct them at socially important individuals (Schel et al. 2013a), potentially to recruit them to a foraging patch. Despite such usage flexibility, the food call's acoustic structure was, as with alarm calls, assumed to be driven by arousal processes. The more excited a chimpanzee was, the more tonal the calls. In 2010 a unique situation allowed a direct test of this hypothesis. A whole group of chimpanzees from the Netherlands were translocated to Edinburgh Zoo in Scotland. This in itself is a rare event, but in addition both groups of chimpanzees had different preferences, and thus differently structured calls, for the same referent: apples. Watson et al. (2015a) capitalized on this opportunity to investigate how food grunt structure was influenced by social integration. Specifically, Watson et al. (2015a) predicted that vocal accommodation may occur between the groups, perhaps to facilitate understanding, aid integration, or both. Interestingly, one year after integration, very little had changed: Dutch chimpanzees had a high preference for apples, Scottish chimpanzees had a low preference, and their food calls reflected this. Social network analysis however indicated that an appreciable degree of modularity still characterized the groups, suggesting they had not yet integrated. Two years later, the picture had changed. Both groups maintained preferences for apples, yet surprisingly, Dutch chimpanzees no longer produced tonal call variants that are commonly associated with preferred foods. Instead, their calls were statistically indistinguishable from the food calls of individuals from the Scottish group (Watson et al. 2015a,b). Dutch chimpanzees had essentially decoupled their preference for the food type (and therefore their underlying arousal) from the fine acoustic structure of their grunts. What's more, social network analyses showed that what were once two groups of chimpanzees, were now one, with as strong bonds between individuals from the different original groups as within the original groups. In line with the predictions of Watson et al. (2015a), vocal accommodation in the functionally referential food calls of chimpanzees had accompanied social integration.

Fischer et al. (2015) criticised these findings, arguing that the results may be better explained through arousal-driven changes in call structure rather than socially mediated acoustic convergence. For example, it may be that arrival in a new enclosure led to heightened levels of arousal in Dutch chimpanzees, which had downstream effects on food call structure. Watson et al. (2015b) rebut this point, highlighting that while the incoming Dutch chimpanzees would undoubtedly have experienced heightened arousal, it seems unlikely that their Scottish counterparts would have been emotionally impervious to such a drastic social change. Hence similar acoustic changes in the Scottish chimp food calls might be expected – yet none were detected. Ultimately, follow-up work (ideally another translocation event), is critical to unambiguously rule out more simple arousal-based explanations. However, what these data do provide is intriguing evidence for social influences on the fine acoustic structure of functionally referential calls, and hence the addition of another plank to the proverbial bridge crossing the gap between animal vocal communication systems and human language.

Conclusions

With the above examples we do not intend to show animal vocalisations are 1:1 analogues of human words, but instead that many of the discontinuities that question the evolutionary relevance of functional referential calls may need revising. When casting the comparative net wide, there does exist evidence for (i) representation of referential call meaning in signaller and receivers, and (ii) decoupling of the arousal state and call structure – arguably one of the key steps for the emergence of a fully arbitrary, symbolic communication system (Townsend et al. 2020). What is missing is consolidation of all of these aforementioned features within a single animal communication system, though two of three ((i) representation on behalf of the signaller and (ii) socially-mediated vocal accommodation) have been demonstrated in chimpanzees. Whether chimpanzees retrieve a mental representation when experiencing food calls is unclear, though it is not beyond the realms of possibility, since similar abilities have been demonstrated in monkeys and parallel work suggests that chimpanzees are capable of representing knowledge (Crockford et al. 2012), and false-belief states (Krupenye et al. 2016) in conspecifics. This nicely illustrates the importance of continued research into the functionally referential calls of animals, not only to better understand the communicative and cognitive capacities of the species in question, but also given their promising ability to shed light on the evolutionary roots of human semantics. We do not suggest this should be done at the expense of research on other non-referential call types, but simply that the more research avenues we keep open and take seriously, ultimately the more likely we are to make progress at unpacking how similar or how different animal vocalisations are to language.

Combinatoriality in animal vocal communication

An increasing body of work on animal vocal systems shows that animals combine acoustic units into higher-order arrangements or sequences, revealing exciting parallels between the vocal combinations produced by animals and humans (Marler 1977; Engesser and Townsend 2019). In the following sections, we provide examples of combinatorial structures that have been described in animals and discuss the extent to which they represent analogues to language's phonology layer (i.e., how phonemes such as /k/, /a/, and /t/ are combined to create meaningful words such as "cat") and compositional layer (i.e., how meaningful words such as "cat" and "hat" are combined to create more complex phrases such as "cat in the hat").

Recombinatorial building blocks of animal calls – a window into language's phonology

Traditionally, comparative work on animals investigating the presence of phonology-like structures outside of human language has (rather than studying the meaning-encoding calls produced by animals as an apparent analogue to human "words") mainly focused on animal songs produced by singing species during mate attraction or territorial defence (Marler 1977; Hurford 2012). In line with this, ample examples show that a diverse number of singing species, ranging from amphibians, birds, cetaceans, and other mammals, recombine smaller meaningless sound elements into larger song-sequences. Although these songs undoubtedly represent some of the most obvious and complex forms of sound combinations in animals, there exist notable differences in the way in which singing species recombine such meaningless elements into songs and the way in which humans arrange smaller sounds into words. Specifically, in the case of animal songs, the resultant sound arrangements do not encode propositional meaning, that is, they lack clear reference and context- and/or function-specificity and do not encode specific meaning. Instead, songs transfer a less concise message that broadly functions in displaying or bonding behaviour, or encode caller quality or identity, whereby the way in which the sounds are arranged generally has little to no impact on the overall message (albeit rearrangements might attenuate or even render a song non-functional) (Marler 1977; Hurford 2012). This is in sharp contrast to how humans recombine smaller meaningless sounds to generate semantically meaningful words, and where slight differences in sound arrangements result in words with different meanings; or put another way, how humans communicate infinite meaning by reusing a finite set of recombinatorial building blocks.

Closer resemblance to the way in which humans use recombinatorial building blocks to encode meaningful information comes from species that produce multi-element calls that are composed of same sound elements, but which encode qualitatively different meanings. In line with this, many chickadee and tit species produce dozens of multi-element calls which are composed of the same sound elements arranged in slightly different ways. However, whether such variation in the Paridae calls also encodes differences in meaning remains ambiguous (Lucas and Freeberg 2007). More compelling evidence comes from work on the vocalisations of chestnut-crowned babblers (*Pomatostomus ruficeps*), where same sound elements also reoccur across different calls, of which two calls are of particular interest. Specifically, these social birds recombine two sounds that are meaningless in isolation – *A* and *B* – to generate two different calls – *AB*-flight and *BAB*-provisioning calls (Engesser et al. 2015; Engesser et al. 2019; Figure 20.1). Observations of these birds under natural conditions and playback experiments under aviary conditions revealed that flight and provisioning calls are context-specific and elicit distinct, ecologically relevant behaviours, that is, they encode qualitatively different meaning and refer to different events. Specifically, babblers produce flight calls during short flights to coordinate movements among conspecifics, and they elicit scanning and movement response in receivers. Provisioning calls stimulate nestling begging during food provisioning and coordinate provisioning by adults. Furthermore, receivers look at the nest upon hearing provisioning calls indicating that individuals relate the call's context- and function-specificity to its typical location of production. To test the recombinatorial aspect of the two calls, that is whether the two calls are each truly composed of distinct sounds which are combined in different ways and reused in

Figure 20.1 **Spectrograms of chestnut-crowned babbler flight and provisioning calls, an analogue to language's phonology**. Both calls are built from recombinations of the same sound elements – *A* and *B*, which are meaningless in isolation, but when arranged into *AB*-flight and *BAB*-provisioning calls encode distinct, context- and function-specific meaning, namely movement and feeding activity, respectively. This is akin to how humans recombine smaller, meaningless sounds (so-called "phonemes") to create meaningful words.

both calls, acoustic analyses and habituation-discrimination experiments were applied. Habituation-discrimination experiments serve to test whether individuals discriminate among presented stimuli by first habituating subjects to a series of repetitions of one stimulus and then switching to another stimulus, testing discrimination via measuring renewal of response behaviours. This demonstrated that, first, each of the two calls are in fact built from acoustically and perceptibly distinct sounds; namely, *A* and *B* were discriminated and hence perceived as different by test subjects. Second, these two distinct sounds are shared between flight and provisioning calls; namely, the *A*s and *B*s were acoustically and perceptibly equivalent when compared across calls. Last, when the sounds were presented in isolation, none elicited differential behavioural responses or flight or provisioning call-related behaviours, supporting that they are meaningless when presented in isolation (Engesser et al. 2015; Engesser et al. 2019).

The chestnut-crowned babbler research therefore demonstrates that animal calls can, like words in human language, be decomposed into a set of smaller, meaningless, recombinant building blocks. Yet, one crucial difference remains: in contrast to the unbounded productivity of language's phonology where a limited number of meaningless sounds can be recombined to create thousands of different meaningful words, the recombinatorial sound reuse in babblers is bounded and appears to be restricted to the generation of only two calls (i.e., *A* and *B* sounds are only recombined into flight and provisioning calls but not reused in any other calls). One hypothesis is that babblers might string these sounds together to generate signals that are simply more salient than the isolated sounds, which, in the end, still serves to increase the number of meanings that can be reliably communicated (Engesser et al. 2015). Despite the difference in productivity, this research finding implies that the ability to recombine smaller, meaningless sounds into meaningful signals has evolved independently in a species very distantly related to humans, and suggests that language's phonology could also have emerged out of similar, unproductive sound-combinations that initially served to enhance the saliency of the signals in use before it then evolved into the fully productive system we have today.

Animal call combinations – a window into human language's compositionality

A number of studies demonstrate exciting parallels between animal call combinations and language's compositional layer and how humans combine meaningful words into phrases to communicate more complex messages that are related to the meanings of the constituent words (note, this is different to phonology, where meaning*less* sounds are combined to create meaning*ful* words). In fact, recent research suggests that this ability is phylogenetically widespread (Engesser and Townsend 2019). For example, banded mongooses (*Mungos mungo*) combine identity-encoding calls with acoustic segments that encode the caller's current behaviour, communicating messages akin to "I, Fred, move" or "I, Fred, forage" (Jansen et al. 2012). In a similar way, Campbell's monkeys (*Cercopithecus campbelli*) produce predator-specific alarm calls which can be combined with an acoustic segment that broadens the alarm calls meaning, for example from "leopard" or "eagle" into "leopard-like" or "eagle-like" (Ouattara et al. 2009). These examples provide exciting data demonstrating the ability to modify the meaning of existing calls by adding meaning-modifying acoustic segments. In these examples, however, the modifying segments (e.g., the behaviour-encoding and the meaning-broadening segment) cannot stand alone, but can only be produced in combination with another call, hence per se do not bear a stand-alone meaning. Although such combinatorial mechanisms can also be found in human languages in the form of affixation, where affixes modify a word's meaning (e.g., "green+ish", with *-ish* being the affix modifying the meaning of *green*), they still differ from the way in which humans combine stand-alone meaningful words into larger phrases and sentences to communicate more complex expressions.

More compelling evidence for compositional abilities outside of humans has been demonstrated in two unrelated passerines, pied babblers (*Turdoides bicolor*) and Japanese tits (Engesser et al. 2016;

Suzuki et al. 2016). Both produce alarm/alert calls which are combined with recruitment calls when encountering terrestrial predators, with the combination inducing a joint mobbing of the predator by conspecifics (Engesser et al. 2016, Figure 20.2). However, there are some differences between the two species. In Japanese tits, stand-alone alarm calls are produced in response to imminent predator threats and elicit vigilance behaviour (i.e., individuals look out for the threat), stand-alone recruitment calls are produced when recruiting mates to the nest and elicit approach behaviour, and the alert-recruitment combination elicits a mixture of both behaviours when mobbing predators (Suzuki et al. 2016). Accordingly, the Japanese tit combination elicits a compound-response of vigilance and approach, being directly relatable to the individual calls (e.g., "look out *and* come here"). In contrast, observations and playback experiments conducted on pied babblers demonstrated that stand-alone alert calls are merely produced when individuals are startled by something unexpected that does not require or elicit any action by conspecifics, such as snapping twigs or other suddenly emerging non-dangerous stimuli. Stand-alone recruitment-calls are produced when individuals lead conspecifics to new foraging sites and receivers respond with a subsequent non-urgent approach towards the caller whilst continuing foraging. Once an individual identifies an imminent terrestrial threat, the signaller combines the alert call with recruitment calls, which leads to a mobbing response by receivers involving high vigilance activity paired with an instantaneous approach to the caller and the threat. Rather than representing a compound-response, these findings suggested that the alert call (despite not eliciting a response when standing alone) adds the threat-indicating context to the recruitment request (e.g., "come here *because of* a threat"), with receivers responding with a threat-adapted approach behaviour to join the caller in the mobbing of the threat. This shows high similarity to basic compositional structures in language, where individually meaningful words are assembled into complex expressions whose meanings are derived from the individual words' meanings and, importantly, their interactional effect.

To summarise, the ability to combine meaningful calls or segments into higher-order meaningful combinations seems to be widespread across the animal kingdom, whereby the closest examples to language-like compositional structures, to date, are found in avian systems. What these findings on animal call combinations suggest is that these combinatorial abilities evolved independently

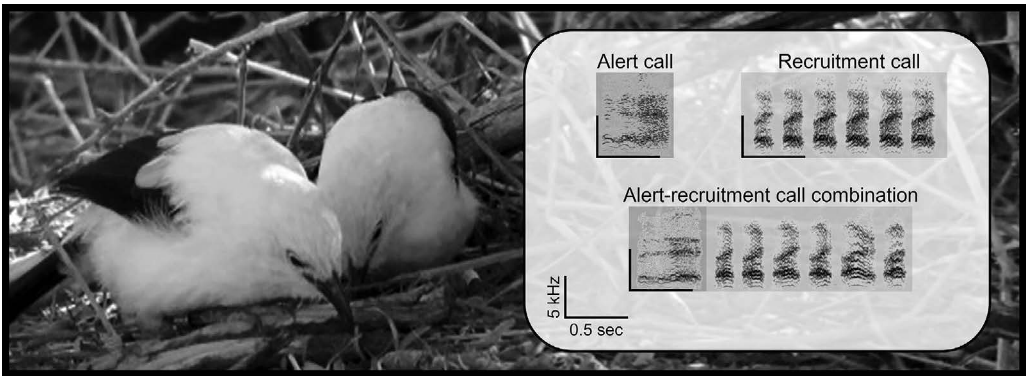

Figure 20.2 **Spectrograms of pied babbler alert-recruitment call combination and the constituent calls, an analogue to language's compositionality.** Alert calls are produced by startled individuals in response to low-urgency stimuli, while recruitment calls elicit approach by conspecifics to new foraging sites. Upon encountering terrestrial predators, both calls are combined into alert-recruitment call combinations which elicit high alertness combined with a threat-adapted approach, suggesting the combination derives its meaning from the individually meaningful component calls with the alert call assigning the threat-indicating context to the approach-soliciting recruitment call. This is akin to how humans combine meaningful words into higher-order phrases whose meanings are related and derived from the component words.

in different clades pointing towards potentially shared selective drivers in their emergence. At the least, the findings raise the possibility that also language's compositional system, which is inarguably more complex in its structures and expressiveness than the call combinations of animals, could have emerged from and built up on similar simple, two-word combinations like the ones found in animals.

Conclusions

The examples provided demonstrate that combinatorial structures are widespread in the animal kingdom, and that they can take diverse forms including analogues to the linguistic structures of human language. However, it is also important to note that whilst we, here, focused on combinatorial structures that resemble language phonology and compositionality, other combinatorial signals exist of which many appear to lack obvious resemblance with the combinatorial structures of human language. Examples include signals where meaning distinction is encoded through temporal differences in series of repeated sound elements, call sequences where meaning is encoded idiomatically or in the transition probabilities between calls, or superficial call combinations that represent read-outs of a caller's current behavioural state that lack a meaningful link between the calls (for further reading see Engesser and Townsend 2019). Despite their difference to human phonology and compositionality, these combinatorial structures still offer intriguing insights into the various ways animals can encode and transmit information. Together, what these comparative data demonstrate is that, like humans, animals can also combine acoustic units into larger vocal structures in order to enhance and amplify their vocal output. Even though these animal examples are far from reaching the complexity and the productivity (i.e., expressiveness) of human combinatorial communication, they suggest that combinatorial capacities in humans and animals might have been driven by similar constraints and selective drivers, in turn allowing us to investigate the evolutionary origins of our own, human, language.

Outlook

For many years animal communication and human language were considered to occupy two opposite ends of the communicative continuum (Rendall and Owren 2013). On the one hand there is the semantically rich and combinatorially productive system in humans, and on the other hand in animals there are vocalisations that are tightly tied to the emotional states encountered and simple in their sequencing. These differences were problematic as they precluded a convincing gradual evolutionary reconstruction of how we got from there (animal communication) to here (human language). However, as illustrated above, an ever-growing body of research confirms that these evolutionary concerns were premature. Rather than representing an insurmountable challenge, communication differences appear to be one of degree rather than kind – a gap that can be bridged (Townsend et al. 2018). More specifically these examples suggest that, firstly, the semantic and combinatorial nature of human language may have its roots in the primate lineage, and secondly, that these basic capacities have evolved independently in more distantly related taxa. This not only makes a gradual evolutionary scenario plausible, but it helps shed light on the evolutionary forces driving such abilities and hence might have been critical during language's evolution.

Whilst considerable progress has been made, outstanding issues still remain when contrasting animal communication and human language. A key evolutionary step allowing a full-blown symbolic communication system to emerge was arguably the complete decoupling of the repertoire from arousal states. Whilst there is evidence that some ape species are capable of such decoupling (Townsend et al. 2020), it remains to be seen if this is restricted to single call types or a more general property of the repertoire or signals more generally (e.g., gestural signals). Flexibility also represents an outstanding issue for combinatoriality in animals. Human language is the epitome of flexible combinatorics with an unlimited potential to generate novel structures, particularly at the compositional level (Engesser et al. 2016). Although current findings indicate that animals can combine meaningless or meaning-bearing units together into larger constructions, how productive such systems are is contentious. Insights will undoubtedly be shed by more long-term systematic investigations into the combinatorial variation of a species and these studies are already under way with promising initial findings.

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21
REASONING

Valérie Dufour

Introduction

Every time an animal solves a problem, scientists can investigate the cognitive mechanisms underlying this resolution. Did the animal use a blind process of learning by trial and error, or, on the contrary, did it use reasoning that enabled it to recognize abstract categories or properties and thus establish relationships between these abstractions? The philosopher Hume (1739, 1748; see also Henderson, 2018) considered that if humans are guided by reason, they do so based on inferences which are themselves based on a principle of similarity (uniformity principle). This is inductive reasoning, by which we predict a new observation based on a series of similar observations previously encountered. For example, we observe that every day at lunch time, many French people have lunch. This knowledge allows us to predict that a French person going out at about twelve is very certainly going to have lunch. However, there is no evidence that this is actually the case, or indeed that the situation will systematically repeat itself in a similar manner. In other words, individuals may infer a situation based on their knowledge or experience, and can hold beliefs about how some premises can lead to a set of consequences. However, counter examples can occur (without challenging the belief), and there is not necessarily an understanding of the ultimate cause or reason for this situation to occur. Inductive reasoning also raises the issue of circularity between experiences and belief, and belief and observations. How can human beings reason by going "beyond the evidence of memory and senses"? This question from Hume has been at the heart of many debates in philosophy and is still influencing the way we envision reasoning today. The process of deduction (Smith, 2003) is often opposed to inductive reasoning. In deduction, the premises allow a person to deduce an explanation from an observation based on logical rules. However, how can we be sure that the premises are true? In everyday decision making, it is more likely that individuals can build beliefs and hypotheses (here the evaluation of the probabilities that an event will occur) based on the frequency at which similar events have been observed. This approach was developed by Bayes (1764): "here a sampling distribution can be taken to be a conditional probability $p(E/H)$, which is known as the probability of certain evidence E in a sample, on the assumption that a certain hypothesis H is true" (cited from Henderson, 2018). In addition, the Bayesian approach considers that $p(E/H)$ can be used to update the probabilities of the hypothesis (H) to be true (posterior probability). Thus, individuals extract rules that can in turn become premises to further evaluate the likelihood that a given event will occur. The advantage of this approach is that premises and predictions are connected by a logical element based on probability.

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The notion of rationality

According to constructivism (for a review see Smith, 2003), decision making is a rational process, in which individuals base their decision on a conscious (deductive) process of reason, in order to maximize their income, according to clear personal preferences. However, some argue that not all decisions can be consciously taken as many individuals make decisions without even knowing that they are doing so. Routine behaviours, situations, or heuristics (simple decision rules that reduce the need to compute all aspects of a problem) can guide individual choices, and may not even require any reasoning (Gigerenzer & Todd, 1999). The term *ecological rationality* has therefore been put forward to describe the role played by the environment (norms, training, habits, society structure, etc.) on individual choices (Todd & Gigerenzer, 2007). Micro-economists consider the notion of *utility,* another approach which, like constructivism, requires logical rules and personal preferences, but does not call upon conscious processes of reasoning. Their goal is to develop models that could be used to predict the behaviour of individuals (customers, financial experts, etc.). In micro-economics, being rational means seeking to maximize the expected utility of a decision (for a review, Caplin & Glimcher, 2014). The decision is based on individual preferences (the revealed preferences approach, Samuelson, 1938), even if these preferences seem absurd to any other individual, such as preferring a small amount of chocolate to a large amount of chocolate. For an individual to be rational, his/her preferences must respect several axioms including preferences that are constant (if A>B, then B is never >A) and transitive (if A>B and B>C then A>C), without possible saturation of satisfaction, and respecting continuity (no abrupt change in preferences when even a small change in probability is made) and independence axioms (no change of preference between two lotteries if a 'medium' term, i.e. a third lottery, is added to each of the two options).

Under risk (i.e. when the probability of each outcome is known), the Expected Utility Theory considers that if an individual makes choices that respect these axioms, then his/her choices can be modelized using a utility function (Von Neumann & Morgenstern, 1944). The desirability of each possible option is obtained by multiplying the utility of the prizes presented in each option by the chances of obtaining them. We can illustrate this with a choice between apples and pears, and imagine, at a given moment, that an apple is three times more attractive than a pear for this individual. Will an individual who prefers apples to pears prefer a lottery with a 50% chance of winning a pear, or a 28% chance of winning an apple? The utility values for the pear are $0.5 * 1 = 0.5$ and for the apple $0.28 * 3 = 0.84$. The individual should choose the option where he has only a 28% chance of obtaining the apple, because the expected utility of this choice remains higher than the expected utility of the alternative.

Allais and Ellsberg paradoxes, and questioning the concept of rationality in humans

Other research has shown that these models were not always adequate to predict decisions, and that judgment "errors" could occur. Depending on how choices are presented, individuals' decisions can become irrational in the sense that they do not respect the fundamental axioms of expected utility theory. A French economist, the winner of the Nobel Prize in Economics Maurice Allais (1953), was able to highlight a certain constancy in the preferences of individuals (and therefore choices); a constancy that is contrary to the axiom of independence. Other paradoxes have been highlighted, such as Ellsberg's paradox (1961), which showed that individuals prefer a risky option (where the probabilities of winning and losing are known) to an option in which the probabilities are uncertain. According to Ellsberg, individuals tend to avoid uncertainty. Other famous economists such as Kahneman and colleagues (1982) have also shown experimentally that many inconsistencies can occur in the choices of individuals. Individuals are sensitive to the way lotteries are presented, and will not make the same choice if the description emphasizes the chances of winning, rather than the chances of losing. This is called the presentation (or framing effect). To illustrate this effect, Kahneman and colleagues presented a problem with two sets of choices that were equivalent in probability but different in terms of the vocabulary used. The problem concerned a treatment program for an unusual Asian disease, and two treatment programs were proposed. Individuals had to choose between program A (200 out of 600 people saved) and program B (1 in 3 chance of saving all people and 2 in 3 chance of saving none). The majority of people chose program A. Then they were offered the same two programs again, but with different vocabulary (Program A: 400 people dead out of 600; Program B: 1 in 3 chance of not dying and 2 in 3 chance of all dying). In this case, the majority of people choose program B. Individuals therefore made different choices depending on how the problem was presented.

Deviations from rational choices in humans

The challenge for micro-economists has therefore been to revise expected utility models so that they could take into account the apparent irrationality of some of these choices. For example, Kahneman and Tversky's work on decision making under risk proposed the theory of perspectives (Kahnman & Tversky, 1979, 1982). In this model, individuals seek to maximize the satisfaction derived from their choices, but they evaluate the different options in a way that takes into account a reference point that is specific to them. This reference point can be their initial wealth or a wealth they hoped to obtain. If someone wins only $10 in the lottery when he or she had hoped to win $100, the actual win may not feel like a win. The authors also showed that there is a pronounced aversion to loss in humans. There is indeed an asymmetry in the response to gains and losses, whereby sensitivity to losses is more pronounced than sensitivity to gains. The weight of a loss is felt 1.5 to 2 times more strongly than a gain. Finally, probabilities are perceived subjectively. For example, if someone plays in a lottery, he or she is subject to a distortion of probabilities when conscious that there is only one chance of winning the jackpot out of about 14 million, since the chances of winning are greatly overestimated while chances of losing the grid price are underestimated (a probability of about 98%).

The endowment effect is another anomaly detected in the expression of choices in humans. This error involves someone attributing more value to a possession than he or she would be willing to pay for it. This type of anomaly, among many others described, is one of the factors that limits the accuracy of economic models in terms of prediction. Kahneman also suggests that individuals are not necessarily capable of very complicated calculations, but will try to simplify the decision by using heuristics, sometimes called statistical intuitions. According to Kahneman (2011) each decision combines the input from two systems in a two-way process (dual process theory): a first system that is intuitive, automatic and fast and involves decision heuristics ('System 1') and a system based on the implementation of explicit rationalization efforts ('System 2'). However, this view is highly debated today (Evans & Stanovich, 2013).

Investigating rationality in animals

In recent decades, biologists, psychologists and neuroscientists have shown a growing interest in studying the evolutionary origins of decision making by looking at decision processes and judgment errors in other species. Many studies have looked at animal responses in economically framed choices. The endowment effect has been reported in capuchin monkeys (Lakshminaryanan, et al., 2008) and has been more widely studied in great apes (Brosnan et al., 2007, 2012; Flemming et al., 2012; Kanngiesser et al., 2011). Overall, great apes are sensitive to endowment when it comes to food (immediate reward) but not when it comes to objects, which they can exchange for food later. Moreover, this effect may be reversible, particularly in chimpanzees (*Pan troglodytes*). Loss aversion was investigated in capuchins (*Sapajus apella*, Chen et al., 2006; Pelé et al. 2014, but see also Silberberg et al., 2008) and orangutans (*Pongo abelii*, Pelé et al., 2014). The presentation effect was also documented in capuchins (Lakshminarayanan et al., 2011). Capuchins, macaques (*Macaca fascicularis*) and orangutans also seem to be subject to the 'hot hand' effect, in which winning leads to more gambling (Pelé et al., 2014). Other studies have attempted to test the responses of species in standard game theory experiments. Game theory investigates how incentives (such as the prospect of a win, for example) influence the decision of agents placed in a strategic environment. An environment is said to be strategic when a player's decision influences the potential winnings or choices of other players. Chimpanzees, for example, were tested in a version of the ultimatum game (Jensen et al., 2007). When human partners play this game, each individual is informed that there will be only one try. The two partners are randomly paired and one receives a sum of money that he or she can divide at will to offer some of it to the other player. The recipient, after viewing the offer, can either accept it (in which case everyone receives the share offered by the terms of the offer) or reject it, in which case no one receives anything. Economic theory suggests that bidders should offer the minimum and receivers should accept all offers because any offer is better than 0. However, this is not what is observed in humans (Sanfey et al., 2003). Most offers constitute 40–50% of the initial sum, and half of the recipients refuse any offers below 20%. Chimpanzees behave differently from humans, and follow the model prediction better (Jensen et al., 2007). However, given that they always accept the offer, it is not clear whether both actors have understood the consequences of a rejection (i.e. that nobody would get anything) and are therefore playing according to this knowledge.

Another example is the trust game, which shows how individuals give their trust, and how this trust is honored in return. In this game, an investor can give part of the money he owns to another individual/partner. The sum received by the recipient (initial amount) is then tripled. In return, the recipient can return part of the money he received to the investor. In humans, investors invest half of the amount that is available to them, while agents tend to return only the initial amount invested by the investor (before the multiplication), or even less. Recently, chimpanzees were tested in an adapted version of this trust game (Engelmann & Herrmann, 2016). The authors showed that more than 60% of the trust demonstrations by the investor were followed by a return by the partner.

Studying how social interaction can affect preferences remains one of the many challenges faced by researchers in biology. When studying decision making in animals, the largest body of research probably concerns decision making under risk (Heilbronner, et al., 2008; Hurly & Oseen, 1999; Kacelnik & Bateson, 1996; Cartar & Smallwood, 1996). Deciding under risk means that the decision-maker has an exact knowledge of the probabilities associated with each outcome. This differs from decisions under uncertainty, defined as those taken with no precise knowledge (Knight, 1921; Luce & Raiffa, 1957). The term "under risk," thus, is not related to a dangerous situation, but indicates that potential outcomes are related to given probabilities rather than certain outcomes.

Decision making under risk and ambiguity

Are some species attracted or averse to risk, and is this attitude optimal in terms of survival? Since animals cannot be given written or oral instructions, protocols traditionally used in economics in humans must be adapted, for example through the use of experiential tests. The principle is as follows: subjects are invited to play a 'game' and experiment with the different aspects of the problem. They are therefore expected to learn the probabilities associated with the options presented to them as the experiment unfolds. A commonly used paradigm is a test of choice between two variances. It consists of offering the subject a series of choices between two options: the safe option, where the reward is obtained in a constant quantity (for example always four grapes) and a risky option, where the reward is obtained in a variable quantity (for example either one or seven grapes) but is equiprobable from one test to the other. On average, therefore, each option offers the same sized reward. Individuals who prefer the certain option are said to be risk averse, those who prefer the risky option are said to be risk seeking, and those who do not express a preference are said to be risk neutral. Many animal species (starlings: Bateson & Kacelnik, 1997; Brito-e-Abreu & Kacelnik, 1999; hummingbirds: Hurly & Oseen, 1999; primates: De Petrillo et al., 2015; Hayden et al., 2008; Heilbronner et al., 2008) have been tested in this way. Results show that several factors influence the attitude towards risk in the species tested, such as the energy budget. In some cases, but not all the time, choices conformed to the predictions from the optimal foraging theory that animals with a severely negative energetic budget should choose the variable option to obtain the highest possible survival outcome. Risk preferences also differ according to how variability is presented in lotteries: if variability is introduced through a manipulation of food quantity, risk aversion is often detected. Risk proneness is more frequently observed if variability is introduced through a delay of access to the resource (Caraco, 1980; Caraco & Chasin, 1984; Kacelnik & Bateson, 1996 for a review). The type of choice, i.e. binary of tertiary options, also leads to a shift in preferences (Hurly & Oseen, 1999). Finally, previous experience influences choices and individuals can also take into account their memory of previous rewards along with the actual expected outcome to make their decisions (Pelé et al., 2014).

Potential flaws of experiential tests

The problem with the experiential tasks is that information needs to be memorized or inferred from previous trials. This may therefore impose different cognitive loads according to the individuals and species tested. Mostly, it would be necessary to evaluate how good animals are at evaluating the odds of outcome (supposedly acquired through repeated exposure to the task). However, this type of post-study control has not been conducted (Bateson and Kacelnik, 1997; Brito-e-Abreu and Kacelnik, 1999; De Petrillo et al., 2015; Hayden et al., 2008; Heilbronner and Hayden, 2013). Additionally, this type of task can reveal whether individuals are attracted by risk (or reject it) but fails to quantify this attitude. In a series of studies, we compared several species of primate to analyse decision making under risk and ambiguity. Compared to other studies, we aimed to analyse individual and species gambling responses using classical models of micro-economics in order to provide estimates for several parameters such as risk aversion, loss aversion and probability distortion parameters. We also sought to facilitate the extraction of odds of outcomes by allowing subjects to visually assess their chances of gains and losses. Non-human primates have skills that are necessary in gambling activities: they can estimate quantities (Beran et al., 2015; Addessi et al., 2008; Silberberg and Fujita, 1996; Call, 2000), add and subtract (Cantlon and Brannon, 2007) and, more importantly, they exhibit self-control abilities (Dufour et al., 2007). The study of decision making under risk requires individuals to be able to understand something about probabilities. Probabilities are conceptually complex (Bernoulli, 1954; Heilbronner and Hayden, 2013), yet they can be intuitively understood. Adult apes (Haun et al., 2011; Rakoczy et al., 2014) also appear to have some grasp of probabilities in various settings. Earlier risk studies have revealed that several species of great apes, macaques and capuchins take the predictability of outcomes into account to maximize their benefits (Pelé et al., 2014; Hayden et al., 2010; Monosov & Hikosaka, 2013; O'Neill & Schultz, 2010; Haun et al., 2011; De Petrillo & Rosati 2019). Other studies have shown intuitive probabilistic inferences in capuchins (Tecwyn et al., 2017) and great apes (Eckert et al., 2017; Racoczy et al., 2014). Thus, non-human primates are equipped with the cognitive skills needed to process odds of outcome.

Decision under risk in an exchange task

In a first study (Pelé et al., 2014), we presented children, great apes (orang-utans) and monkeys (long-tailed macaques and capuchins) with a risky food exchange task. We first trained individuals of each species to exchange one small piece of cookie for a piece of cookie of a larger size with an experimenter. Then, during testing, we gave the subject an initial medium-sized piece of cookie and showed them a lottery, that is, a tray of six aligned cups, each containing either a small, middle-sized or large reward (Figure 21.1). Individuals were then invited to exchange their initial piece of cookie

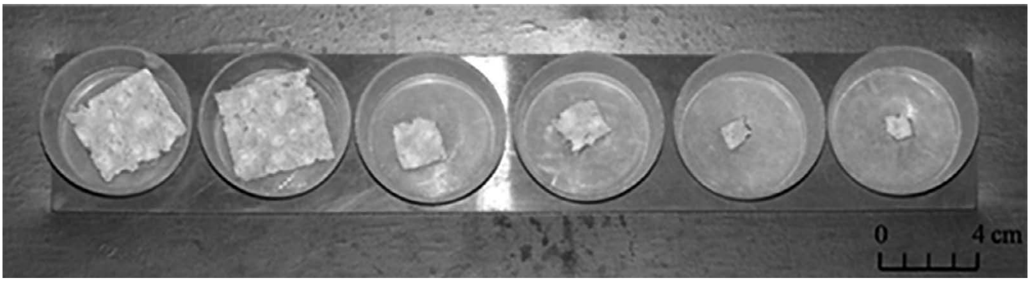


Figure 21.1 A tray of six plastic cups containing different sized pieces of crackers. Two cups contain one piece of large cracker (left positions), two cups contain one piece of medium cracker (middle positions), and two cups contain one piece of small cracker (right positions). Individuals can see that there is a 33% chance of success, and a 33% chance of loss. Large size: 4 x 4 x 0.5 cm. Medium size: 2 x 2 x 0.5 cm. Small size: 1 x 1 x 0.5 cm.

for the content of one of the six cups (randomly assigned). Thus, keeping (and eating) the initial piece of cookie was the safe option, and gambling in the lottery was the risky option. The contents of the cups were modified from one lottery to another to provide 18 different lotteries for which the odds of winning or losing were visually assessable (e.g., five cups holding a smaller reward and one cup holding a larger one, making it a 1/6 chance to win). Thus, by visually inspecting the contents of the cups, individuals could evaluate with one glance their odds of winning a larger cookie, or of losing (by obtaining a smaller cookie than the one they initially had).

In this first study, we comparatively tested orangutans (*Pongo abelii*), long-tailed macaques (*Macaca fascicularis*), and capuchin monkeys (*Sapajus apella*). The lotteries were presented in such a way that the chances of winning progressively decreased throughout the study. We showed that the three species tested decreased their gambling rates when the expected value of lotteries decreased, as described in the expected utility theory (Von Neumann & Morgenstern, 1944). The analysis of choices using stochastic dominance showed that macaques were risk prone whereas capuchins and orangutans were risk averse. We detected responses comparable to the hot-hand effect. By implementing models based on the cumulative prospect theory, we found that capuchins and orangutans exhibited probability distortion and loss aversion, which were not systematically found in macaques.

Importantly, the gradual decrease in the chances of winning probably facilitated the extraction of information about odds. In addition, subjects were tested several times in a row for a given lottery before moving on to tests in further new lotteries. This probably helped to quickly decide on a course of action for each new set of "same lottery" trials (18 trials in a row for a given lottery before moving on to the next lottery with a lower expected value). We suggested that this design probably limited the cognitive focus needed to compute the odds of winning or losing and facilitated the memorizing of the decisions and outcomes for a given lottery.

Effect of increasing cognitive load on decisions under risk

In a second study, we investigated whether individuals would still make efficient decisions if this facilitating factor was removed. Individuals from four ape species (chimpanzees, bonobos – *Pan Paniscus*, gorillas – *Gorilla gorilla*, and orangutans) and two monkey species (Tonkean macaques – *Macaca tonkeana*, and capuchin monkeys) were tested. We proceeded in a very similar manner except that the order of presentation of the lotteries was randomized from one trial to the next. This was done to limit the possibility that an individual would learn about the odds through consecutive repetition of the same lottery trials during the study. To know about the odds associated to each outcome, subjects needed to pay attention to the content of the cups at every single trial. As in the previous experiment, we analysed responses within the framework of the Expected Utility Theory and Cumulative Prospect Theory (Broihanne & Dufour, 2018). We detected risk aversion in bonobos and chimpanzees with coefficients that were close to those measured in human adults. We did not detect loss aversion but this may be due to excess heterogeneity in the data. As in humans, attitudes are not necessarily constant, and they may change according to context and framing (Lévy-Garboua et al., 2012). Between-species homogeneity in the coefficients expression may help shed more light on evolutionary pressure (if, for example, bonobos are always the most risk-averse of all species, and macaques and orangutans are always the least risk-averse). This is one of the strengths of our experimental design. The observation that bonobos and chimpanzees are closer to humans than any other species could indeed reflect a common evolutionary process that affects how species evaluate the opportunity to gamble one thing for another. This perspective requires further investigations.

In this second study, a first glance at the data showed that gambling rates increased as expected values increased, indicating that subjects appeared to pay attention to the probability distributions that were proposed before they gambled. Indeed, they did so with remarkable precision. However, all species gambled far more than they should have in one of the lotteries tested, which partially contradicts the notion that their decision was solely based on probabilistic evaluation. We sought to understand this response by conducting a complementary analysis to investigate the possibility that individuals relied on heuristics to make their decisions. Heuristics are simplified decision rules that help individuals to deal with situations that require a high cognitive investment (Rieskamp & Hoffrage, 1999; Brandstätter et al., 2006). Here, randomizing the lottery presentation order leads a large number of individuals in all tested species to predominantly use a *maximax* heuristic (Broihanne et al., 2019). In this heuristic, individuals tend to gamble as soon as there is at least one chance to win more than they already possess (i.e. as soon as they see at least one large cookie in the cups) whatever the risk (i.e. disregarding potential losses). These results suggest optimistic behaviour. The maximax heuristic is sometimes observed in human managerial and financial decision making, where risk is ignored for potential gains, however low they may be. This suggests a shared and strong propensity in primates to rely on heuristics whenever complexity arises in the evaluation of outcome odds.

Effect of uncertainty on decisions rules in an exchange task

Our most recent study (Romain et al., 2021) used the same task, but also exposed individuals to ambiguous options. We expected individuals to make use of simple decision rules rather than attempting to evaluate the odds of winning or losing, thus expressing ambiguity aversion (with only partial information about the odds). We also investigated the role played by different levels of information about odds in monkeys and great apes. In this modified version of the exchange task described above, subjects could gamble a food item in their possession in exchange for the contents of one of the six cups displayed in front of them. Each cup contained either a larger or smaller amount of food than the amount possessed by the subject. The decision was made under risk when the subjects could visually assess the odds of winning and losing (for example, they had three chances out of six to receive more food if three cups contained a larger cracker and three cups contained a smaller cracker than the one they already possessed). Ambiguity was implemented by covering some of the cups (Figure 21.2). We manipulated the contents of the cups to offer lotteries with varying gain predictability. By changing the presence and location of the covers, we could vary the amount of information available so that subjects made their decision under four conditions: *i.* risky lotteries, where subjects could see all the potential outcomes; *ii.* predictably advantageous lotteries, where subjects could not see but could infer (according to how the lotteries were set up) that the covered cups contained large rewards; *iii.* predictably disadvantageous lotteries, where subjects could not see but could infer that the covered cups contained small rewards, and *iv.* ambiguous lotteries, where subjects could not guess the exact probabilities associated to potential outcomes. Given our results in the previous studies and the findings described in the literature, we expected subjects to either reject

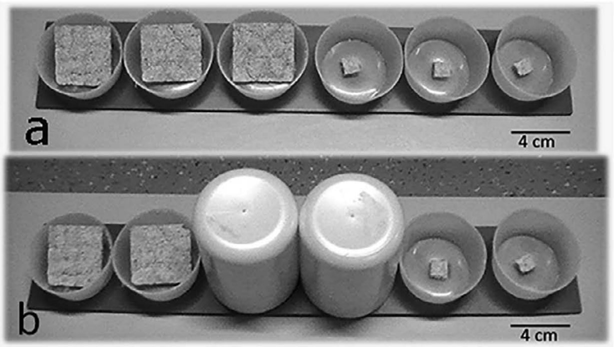
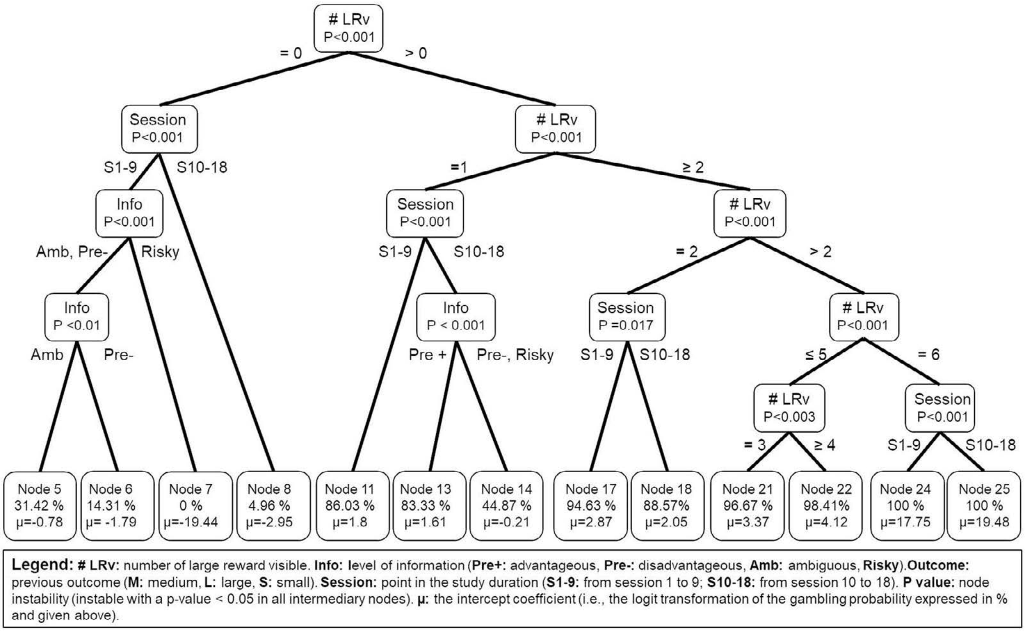


Figure 21.2 Example of two lotteries presented to the subjects. (a) A tray of six plastic cups containing pieces of crackers that are either larger or smaller than the food item they have already been given. In this risky lottery, three cups contain a large cracker (cups 1–3, left) and three cups contain a small cracker (cups 4–6, right). There are no covers and individuals can see that there is a 50% chance of success. (b) In this ambiguous lottery, there are two covers in the middle that can each hide small or large crackers. Individuals cannot precisely estimate their chances to win. Large crackers: 4 x 4 x 0.5 cm. Small crackers: 1 x 1 x 0.5 cm.



Legend: **# LRv:** number of large reward visible. **Info:** level of information (**Pre+:** advantageous, **Pre-:** disadvantageous, **Amb:** ambiguous, **Risky**).**Outcome:** previous outcome (**M:** medium, **L:** large, **S:** small). **Session:** point in the study duration (**S1-9:** from session 1 to 9; **S10-18:** from session 10 to 18). **P value:** node instability (instable with a p-value < 0.05 in all intermediary nodes). **μ:** the intercept coefficient (i.e., the logit transformation of the gambling probability expressed in % and given above).

Figure 21.3 Decision tree for the orangutans showing the order of importance of each variable in the final decision. The number of large rewards visible (# LRv) is the first variable that plays a role. Orangutans gamble more than 50% of the time for lotteries with at least one large visible reward (1LRv, from node 11, except for node 14). The level of information also plays a role at 0 LRv, i.e. when no large cookies are visible (especially at the beginning of the study), and 1 LRv lotteries (especially at the end). This decision tree shows that orangutans gamble more at lotteries that are more likely to provide large rewards under the covers (nodes 5 and 13). The point in the study duration can also play a role for 2LRv. Extracted from Romain et al. 2021.

ambiguous lotteries altogether (by only gambling in lotteries without covers, i.e. risky lotteries), or to ignore ambiguity and gamble based on visible information through simple heuristics (such as counting the number of large visible rewards, and/or by using maximax heuristics). However, this study showed that orangutan and chimpanzee individuals considered the level of information about odds, responding differently to contexts in which they could predict their odds of gains and those in which they could not (Figure 21.3). Unlike the two previous hypotheses, this third alternative is more complex because it requires subjects to build correct expectations about the content of the covered cups in predictable lotteries. An innovative statistical tool based on decision trees with repeated measures allowed us to highlight the decisional steps involved in each species. In chimpanzees and orangutans, the decision was based on the combination of rules, which resembles the process of conditional probabilities assessment described in humans. In economics, making inferences involves a computation of conditional probabilities using Bayes' rule, a cognitively demanding task. To our knowledge, this is the first time that the use of conditional probabilities has been demonstrated in an ambiguous decision-making context in other animals.

Conclusion

Interestingly, most tested species also show errors of judgment that are sometimes detected in human decisions. However, more comparative studies are required to better understand the origins of these similarities between species. At the beginning of this review, we mentioned that humans could extract logical rules from the situations they are familiar with. These rules can become premises to help individuals predict the likelihood that another event will occur. Our study showed that two species of great apes chose/decided in a way that suggests they used a similar type of reasoning when faced with ambiguous options. Like humans, other animal species can establish logical (probabilistic) relationships between two events. However, while individuals may have the correct intuition about assessing odds of outcomes in risky or ambiguous situations, we still do not know if they can identify a causal value in a chain of events and make hypotheses about the world. Some studies suggest that animals can recognize a causal agent (a real entity), but research to date still fails to convincingly demonstrate that animals can use abstract notions or invisible forces to explain what they observe.

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22

DECEPTION IN ANIMAL COMMUNICATION

Tom Flower

Deception

In southern Africa's Kalahari Desert a bird, the fork-tailed drongo (*Dicrurus adsimilis*), sits on a thorn bush overlooking a group of foraging meerkats (*Suricata suricatta*). The meerkats benefit from drongo presence because they can respond to the loud alarm calls given by the drongo and flee to cover when predators approach. However, the drongo is benefitting from this interaction as well: it is watching a meerkat digging in the sand, and the meerkat has found a small lizard. The drongo makes an alarm call and the meerkat flees, yet there is no predator and the drongo swoops down to collect the abandoned lizard. The drongo has deceived the meerkat, and in so doing gained an otherwise unobtainable prize (Flower, 2011; Flower et al., 2013).

Such fascinating acts of deception occur throughout the natural world from bacteria that coat themselves in sugar to evade detection by host immune systems, to soccer players diving to be awarded a penalty kick (Coyne et al., 2005; David et al., 2011). In fact, deception is integral to interactions between organisms wherever one individual can benefit by manipulating the behaviour of another (Dawkins and Krebs, 1978; Maynard Smith and Harper, 2003; Searcy and Nowicki, 2005). In this chapter, it would be impossible to address all known examples of deception across different modalities (vision, olfaction etc.), behaviour types (foraging, predation, reproduction etc.) and taxa (Mokkonen and Lindstedt, 2016). However, using an evolutionary perspective we can gain key insights into the universal features of deception, how deception persists within communication systems, the coevolutionary processes between deceivers and the deceived, and the consequences for the evolution of complex deceptive behaviour and the cognitive mechanisms responsible.

I therefore begin this chapter with an overview of deception in biological systems, considering how and why deception occurs before identifying the contexts of deception. I then explore the central role of deception in the development of modern communication theory; first when biologists worked to establish why communication is honest given that selfish signalers may benefit by manipulating receivers, and then to establish how deception can exist if communication is honest. I follow with discussion of how selection operating on both receivers to better avoid deception and deceivers to better manipulate others, has shaped deception systems through coevolution. Using examples from research on fork-tailed drongos, I further explore how such coevolution has generated flexible behavioural tactics, and even cooperation between deceivers and receivers. Finally, I emphasize future directions for research on the cognitive mechanisms underpinning deception and address the implications of flexible deceptive tactics for the evolution of intentionality/theory of mind and by extension, social cognition.

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How and Why Does Deception occur?

Deception occurs where a deceiver manipulates receiver perception, causing a misalignment of the real state of the environment and the receiver's perceived representation, to the receiver's cost and the deceiver's benefit (Carazo and Font, 2014; Mokkonen and Lindstedt, 2016; Searcy and Nowicki, 2005). Deception can persist, so long as the benefit receivers gain from honest information ensures that it still pays for them to attend to the information (Maynard Smith and Harper, 2003). This evolutionary definition of deception combines both the functional outcome in terms of costs and benefits and therefore the direction of natural selection, as well as the mechanism and therefore how selection will act on both deceivers and receivers. Consequently, it unifies diverse deceptive acts including manipulation of either signals or cues (Table 22.1) from the social and physical environment, or the activation versus inhibition of receiver behaviour. For example, subordinate monkeys conceal food items from dominants thereby disguising a *cue* (Hare et al., 2000), while chicks increase begging *signal* intensity to exaggerate their hunger (Godfray, 1995; Trivers, 1974). Similarly, deception can involve either activation or inhibition of receiver behaviour (Table 22.1) (Mokkonen and Lindstedt, 2016). Death adders (*Acanthophis antarcticus*) attract lizard prey by moving their tails to mimic small invertebrates such as worms, termed 'caudal luring', thereby *activating* lizard feeding behaviour (Nelson et al., 2010). By contrast, edible butterfly species avoid being eaten by mimicking the warning coloration of inedible poisonous butterfly species, thereby *inhibiting* predator feeding response (Platt et al., 1971).

Table 22.1 Summary of deception terms

Term	*Description*
Communication	Action or characteristic of one individual that influences the behaviour, behavioural tendency or physiology of another to the benefit of both on average. Specifically, communication involves the production of signals which are the outcome of interaction between signalers and receivers where both parties, at least initially, gained benefits from the signal on average.
Signals	Characters under selection because they provide information to receivers that is reliable on average and modifies receiver behaviour.
Cue	Information provided to receivers as a byproduct of another organism's activity.
Deception	A deceiver manipulates receiver perception, causing a misalignment of the real state of the environment and the perceived representation by the receiver to their cost, and the deceivers benefit.
Incomplete honesty	Signals produced in their original context, but which exaggerate or attenuate information content, such that there is mismatch between signal information and reality.
Categorical deception	Signals produced in a context different from the honest context in which the signal evolved, such that there is no correspondence with reality.
Mimicry	Evolved resemblance of a mimic to a model resulting from receivers failing to discriminate mimic and model to the benefit of the mimic. Mimicry may be deceptive e.g., Batesian, aggressive or sexual mimicry, but is often non-deceptive e.g., Mullerian mimicry
Tactical deception	Production of a signal from an organism's honest repertoire in a dishonest context.
Intentional deception	Intentional attempt to create false beliefs in others
Machiavellian Intelligence Hypothesis	Evolution of cognitive mechanisms resulting from manipulation of complex social interactions and the detection of manipulation.

Contexts of Deceptive Signaling in Communication Systems

The manipulation of signals that have evolved within communication systems is undoubtedly the most common form of deception and accounts for many of the most familiar examples including deception in human language (Dor, 2017). For clarity, communication systems are the outcome of interactions between signalers that provide information to influence receivers, to the benefit of both the signaler and the receiver on average (Table 22.1). Deceptive signalers are able to exploit receivers within communication systems in two fundamentally different contexts: (i) Incomplete honesty where a signal is used deceptively in its original evolutionary context, but the signal is either exaggerated or attenuated by the signaler, or (ii) categorical deception where a signal is used in a new context different from that in which the original honest signal evolved (Figure 22.1) (Carazo and Font, 2014). Distinguishing these is important because incomplete honesty is likely inherent within all signaling systems where individuals have shared, but non-identical interests and ultimately speaks to our understanding of how signals evolve to be stable and honest (Dawkins and Krebs, 1978; Maynard Smith and Harper, 2003; Searcy and Nowicki, 2005). By contrast, categorical deception is effectively parasitic on existing signaling systems; the interests of signaler and receiver are not aligned, and receivers would not respond unless an honest counterpart signal provided benefits.

(i) Incomplete honesty

To illustrate incomplete honesty, let us consider the famed sexual cannibalism of praying mantids, in which females eat males during copulation (Barry et al., 2008). Praying mantis females attract males with pheromones and well fed, high-quality females both produce more pheromones and are less likely to consume males than most females (Barry et al., 2008). However, very-poor-quality females deceive males, because they produce similar pheromone levels to high-quality females, yet offer lower reproductive success for males and are highly likely to eat them (Barry, 2015; Barry et al., 2008).

(ii) Categorical deception

Categorical deception often involves mimicry (Table 22.1) to: (a) reduce predation (Batesian mimicry) as observed in palatable butterfly species mimicking unpalatable species (Platt et al., 1971), (b) enable prey capture (aggressive mimicry), such as caudal luring by snakes (Nelson et al., 2010), or (c) increase mating opportunities (sexual mimicry), for example, male mourning cuttlefish (*Sepia plangon*) mimic females to gain access to females guarded by larger males (Brown et al., 2012). Categorical deception can also occur when individuals capable of producing an honest signal flexibly produce the same signal in a dishonest context, as observed in drongo's true and false alarm call production (Flower, 2011). Functionally, this is tactical deception, but it is important to distinguish this from cognitively 'intentional' tactical deception (Table 22.1), requiring use of an honest signal in a dishonest context to intentionally cause another to register a false belief (Mitchell and Thompson, 1986). We will return to discuss this point later when considering the cognitive outcomes of interactions between deceivers and the deceived.

Honesty and Deception in Animal Communication

In communication systems, signalers are selected to manipulate receivers to their advantage and receivers are selected to respond to signals only where they provide reliable information (Dawkins and Krebs, 1978; Maynard Smith and Harper, 2003). In some communication systems, signaler and receiver interests are near perfectly aligned, such as the waggle-dance of honey bees (*Apis mellifera*)

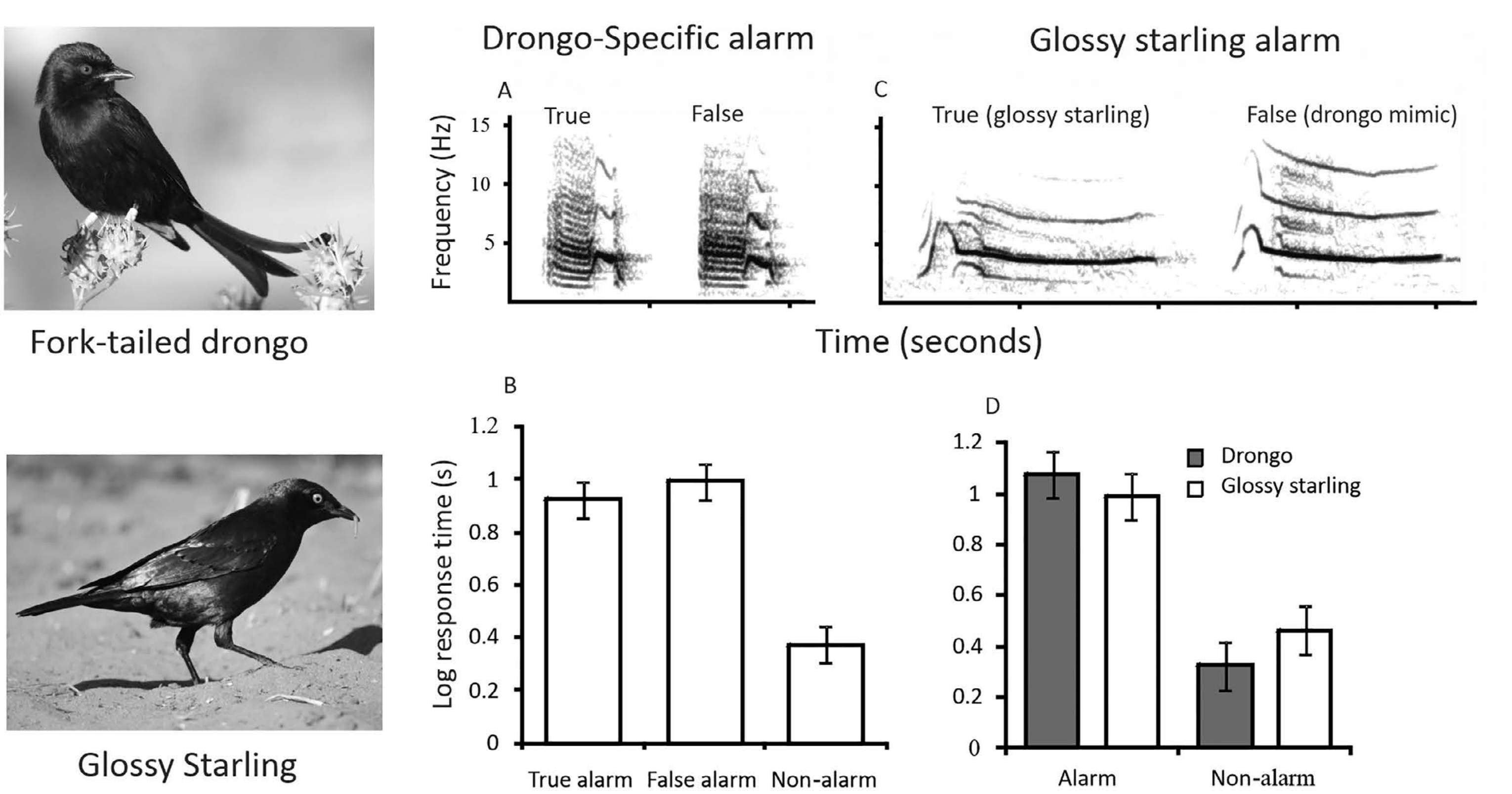

Figure 22.1 Deceiving a Meerkat. Flower (2011) identified key criteria to demonstrate deception, showing that (A) Drongo-specific alarm calls produced by drongos were the same in both true predator and false food theft contexts, and critically meerkats (B) fled in response to both true and false drongo-specific alarms, more than to control non-alarm calls. To demonstrate deceptive mimicry, Flower additionally showed that (C) true alarm calls made by glossy starlings at predators were the same as some false alarm calls made by drongos in food theft contexts and meerkats (D) fled in response to both true glossy starling alarms and false mimics by drongos, more than to control non-alarm calls.

(Von Frisch, 1967). However, more typically, signaler and receiver interests are not aligned and signalers will produce incompletely honest signals that manipulate receivers to the signaler's maximum benefit, even where this is costly to the receiver (Dawkins and Krebs, 1978; Maynard Smith and Harper, 2003). Herein lies the central paradox of communication; how can signals evolve and persist if incomplete honesty exists?

Research over the past 50 years has reached the consensus that signal honesty is maintained because receivers respond to costly signals that enforce reliability (Maynard Smith and Harper, 2003; Searcy and Nowicki, 2005). Signal costs may be implicitly linked to '*indices*' of body condition, such as physical size determining vocalization frequency in males (Davies and Halliday, 1978). Alternatively, costs may result from selection by receivers for exaggerated signals (termed '*handicaps*'), as occurs in sexual selection for traits such as the peacock's tail, whose quality correlates with individual condition (Johnstone, 1995; Petrie, 1994; Zahavi, 1975). Finally, reliability may be enforced by costs of signal probing, for example threatening displays which signal aggressive intent and incur their cost when they are challenged (Laidre, 2009). Given that enforcement mechanisms maintain honest signaling, we are then left to query how deception can occur.

Fundamentally, deceptive communication persists because it can still benefit receivers to respond to signals on average. This occurs where the benefits of responding to honest signals are greater than the costs of responding to deceptive signals (Johnstone and Grafen, 1993; Maynard Smith and Harper, 2003). Extrapolating to include deception via cue manipulation: deception can persist where the benefit of acting on perceived information is greater than the costs of ignoring or failing to register the perception. For example, if we consider drongo alarm communication, it may well pay for meerkats and other animals to respond to alarms where the benefits of avoiding being eaten by a predator far exceed those of losing a food item (Flower, 2011). Nevertheless, deceived individuals are under intense selection to avoid deception and should adjust their response depending upon variation in the current costs and benefits of responding. Indeed, selection on receivers to detect deception, and consequently for deceivers to evade detection, has resulted in some of the most exquisite examples of coevolution, which provide unique insight into the evolution of communication tactics.

Deceptive Coevolution: Receiver Response and Deceiver Counter-tactics

Receiver response to deception may be predicted to depend upon: (i) receiver capacity to discriminate honest versus deceptive perceived states, (ii) the intrinsic benefit of responding to the honest perception (versus costs of responding to the dishonest perception), and (iii) the overall frequency of honest versus dishonest information in the environment (Maynard Smith and Harper, 2003; Mokkonen and Lindstedt, 2016; Wiley, 1994). In turn, receiver response places strong selection pressure on deceptive signalers to adopt counter-tactics to enhance deception (Figure 22.2). To illustrate the coevolutionary outcomes, let us examine the three processes affecting receiver response and their consequences for deceiver counter-tactics,

(i) Discriminating between honesty versus deception

A receiver's ability to discriminate between deceptive and honest perceived states will depend upon the perceptual overlap in the characteristics of signals and/or contextual cues produced by deceivers (Searcy and Nowicki, 2005; Wiley, 1994). Selection will operate on receivers to more accurately differentiate deception, while deceivers are selected to more accurately match honest perception (Brooke and Davies, 1988; Dawkins and Krebs, 1979). This process is beautifully illustrated by the interactions between brood parasites and their hosts. Brood parasitic birds such as cuckoos lay their eggs in the nests of host species which then raise the parasitic chick, while the hosts own chicks are typically killed or suffer reduced fitness. Consequently, hosts recognize and eject eggs dissimilar to their own, and are better at recognizing more dissimilar eggs; in response brood parasites have

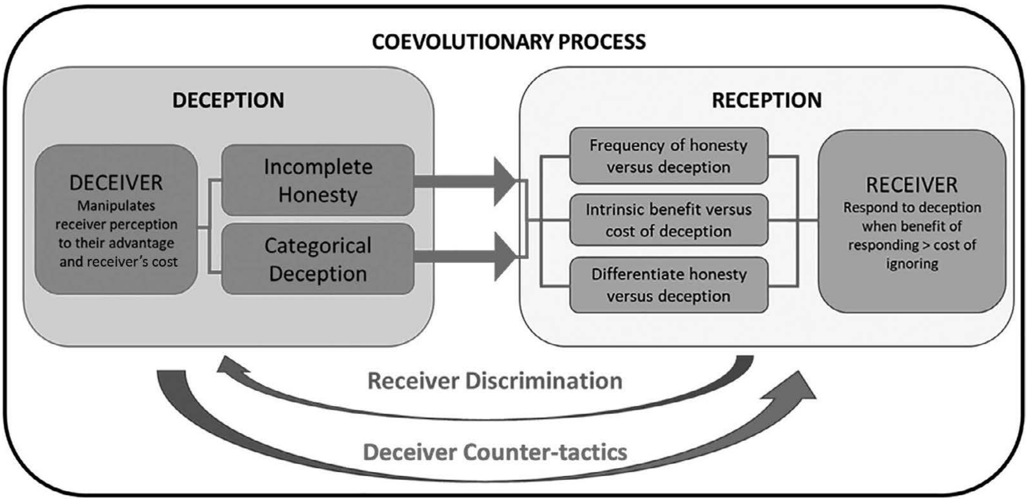

Figure 22.2 Coevolutionary interactions between receiver's cost and receivers highlighting contexts of deception, selection on receivers to reduce deception and consequent selection for deceiver counter-tactics.

coevolved to produce eggs better matching their host's, thereby reducing egg rejection (Brooke and Davies, 1988; Spottiswoode and Stevens, 2012, 2011).

(ii) Intrinsic benefits versus costs of deception

For receivers, when there are high intrinsic benefits of responding to a perceived state of the environment, or the costs of being deceived are low, deception is more likely. Nevertheless, receivers vary their response depending upon intrinsic benefits and deception costs as illustrated by the great tit (*Parus major*). Great tits are more likely to avoid both distasteful model prey items showing warning coloration and their deceptive mimics, when the model is more distasteful (intrinsic benefit of the signal) (Lindström et al., 1997), *and* when they are relatively satiated (cost of deception) (Rowland et al., 2010).

Typically, it is beyond the scope of deceivers to manipulate intrinsic benefits or deception costs. Intrinsic benefits are determined by the context of the honest signal and deception costs are precisely the benefit that deceivers are selected to enhance e.g., avoidance of being eaten for a Batesian mimetic butterfly (Platt et al., 1971). However, species that are tactically deceptive (Table 22.1) could increase receiver response to deceptive signals by enhancing the intrinsic benefit of their honest signaling, or by employing deception only when there are low costs to receivers from failing to detect deception. We will return to explore these possibilities later within a drongo case study.

(iii) Frequency of honesty versus deception

Where deception frequency increases relative to that of the honest counterpart, receivers decrease their response to deception (Maynard Smith and Harper, 2003). This frequency-dependence of deception is well illustrated by research on the venomous coral snake (*Micrurus folvius*) and its Batesian mimic, the king snake (*Lampropeltis triangulum elapsoides*), showing that in regions king snakes are not sympatric with coral snakes, predators no longer avoid king snakes and instead attempt to eat them (Pfennig et al., 2001). However, frequency-dependent constraints can be reduced by deceiver polymorphisms – where different morphs mimic different honest models (Mallet and Joron, 1999). The benefit of new or rare morphs is beautifully illustrated by brood parasitic cuckoo finches

(*Anomalospiza imberbis*), and their host the tawny-flanked prinia (*Prinia subflava*). Selection favors prinia individuals that produce new egg colour polymorphisms aiding discrimination and rejection of cuckoo finch eggs, but cuckoo finches that then produce matching new egg polymorphisms are under positive selection (Spottiswoode and Stevens, 2012). This process has led to corresponding variation in the frequency of each deceptive egg polymorphism over time in relation to the abundance of the matching honest model (Spottiswoode and Stevens, 2012). Consequently, the selective advantage of new deceptive phenotypes is only temporary, resulting in ongoing coevolution between deceiver and deceived (Maynard Smith and Harper, 2003).

Flexible Deception

Most deceptive species display a fixed deceptive phenotype, but some can flexibly vary their deceptive phenotype which opens new possibilities for the evasion of receiver detection. Specifically, flexible individuals could employ deception such that it is harder to discriminate from honesty or expand opportunities for deception in new contexts. Additionally, species capable of tactical deception (Table 22.1), may adjust the production of honest or deceptive information. To illustrate these advantages consider the Horsfield's bronze cuckoo (*Chrysococcyx basalis*), another brood parasite whose chicks tune their begging calls to mimic those of their host species, thereby enabling individuals to parasitize different hosts (Langmore et al. 2003; Langmore et al. 2008). Similarly, the araneophagic spider *Portia fibrianata*, which stalk and prey on other spider species, may either pluck on their prey's webs in patterns that camouflage the *Portia*'s movements as wind, mimic the struggling of captured prey, or even mimic the plucking of males to enable capture of female spiders (Jackson and Cross, 2013). Furthermore, it has been suggested that *Portia* attend to feedback from their prey's behaviour to tune their deceptive signaling (Jackson and Cross, 2013). Flexible deception, incorporating attendance to receiver behaviour, therefore enables manipulation of receiver perception to better match honest signals and exploit perceived states that have higher intrinsic value to receivers.

Deceivers could even flexibly moderate deception frequency to maintain receiver response where tactically deceptive individuals repeatedly interact with receivers that can identify and discriminate between deceivers. Cleaner wrasse (*Labroides dimidiatus*) cooperatively feed on client fish parasites, yet may also bite their clients to obtain their preferred food, skin mucus (Bshary, 2002). Clients of cleaner wrasse often queue for service and exert partner control by leaving if they observe a cleaner wrasse bite another fish (Bshary, 2002). Consequently cleaner wrasse strategically clean small fish and then bite the more profitable large fish in the queue (Bshary, 2002). In this scenario, the cleaner's cooperation with small fish is effectively a deceptive signal of cooperative intent, that facilitates cheating (Brosnan et al., 2010).

Together, the preceding examples illustrate how flexible deceivers maintain receiver response through manipulation of discrimination, intrinsic costs/benefits and the frequency of deception. To further explore the specific advantages flexible deception provides in relation to the evasion of receiver detection, I now take a deeper dive into the behaviour of the Fork-tailed drongo.

Fork-tailed Drongo: a case study in flexible deceptive tactics

Fork-tailed drongos are medium/small birds common throughout southern Africa, where they are most commonly seen hawking flying insects in the air or gleaning invertebrates and small vertebrates from the ground. During cold winter months when aerial prey are less available, drongos also follow other species, particularly ground foraging and group-living species that disturb drongo prey, much as seagulls and crows will follow a plough through a field (Flower et al., 2013). Perched above these host species, drongos are frequently the first to alarm at predators, and host species consequently eavesdrop on drongo alarm calls, as well as those of many other species in their environment, to gain early warning of danger and avoid predation (Magrath et al., 2015). As described at the start of this chapter, drongos can turn their alarms to a more nefarious purpose, by making deceptive alarm calls to scare individuals and steal their abandoned food. However, there is more to this story: in addition to producing their own drongo-specific alarm calls, drongos can mimic the alarm calls of other species to steal food. In the Kalahari Desert, drongos are known to follow at least 25 different species and have been recorded mimicking over 45 different alarm call types during food theft attempts.

Using the drongo as an example, I now illustrate what deception benefits are provided by the ability to (i) vary a deceptive signal, (ii) vary deceptive context, and (iii) tactically produce honesty versus deception. Additionally, I consider whether repeated interactions with host species may ultimately favor cooperative tactics that enhance deception, yet also benefit receivers, resulting in a transition from parasitic to mutualistic relationships.

(i) Variation of a deceptive signal

By varying their deceptive signal, deceivers may exploit signals more likely to deceive hosts. Indeed, when attempting to steal food, drongos most often mimic the alarm calls of their host species and experimental playback of calls to one host, the pied babbler (*Turdoides bicolor*), reveals pied babblers are more likely to flee in response to mimicry of their own alarm calls than drongo-specific alarm calls (Flower et al., 2014). Consequently, flexible mimicry likely allows exploitation of an honest signal with higher intrinsic value to different receivers, and which may be more frequently honest. Surprisingly, mimicry of the babbler's own alarm calls or other species alarm calls was equally likely to cause pied babblers to flee, perhaps because pied babblers are better able to discriminate deceptive mimicry of their own alarms. Nevertheless, host mimicry is likely an effective heuristic rule of thumb that allows drongos to vary their alarm calls to best exploit different hosts (Hutchinson and Gigerenzer, 2005).

By varying their deceptive signal, deceivers could additionally maintain deception where frequently produced deceptive signals no longer fool receivers. Corroborating this prediction, when pied babblers are repeatedly played alarm calls featuring either drongo-specific or mimetic call types, the pied babbler's response to the corresponding alarm call declines. Yet when the alarm call is switched to a different type (either drongo-specific to mimic alarm call or vice versa), pied babblers then increase their responsiveness (Figure 22.3). Natural observations of drongos confirm that they exploit this propensity by tactically changing alarm calls between food theft attempts, and more often change when hosts did not respond to a previous deceptive alarm call (Flower et al., 2014). These results indicate that drongos use their capacity for vocal mimicry to vary deceptive signals and evade frequency-dependent constraints during repeated interactions with a specific host species (Flower et al., 2014). Such behaviour is possible because drongos are not only flexible in their communication tactics, but also able to attend to feedback from receiver behaviour.

(ii) Variation of deception context

Flexible deception enables deceivers to target contexts where receivers are most likely to be deceived. For drongos, one means of varying deception context to achieve high payoffs is through targeting of more vulnerable species, for whom there is high intrinsic value in the extra predator vigilance provided by a drongo's honest alarm calls. Consistent with this prediction, drongos favor flocks of sociable weaver (*Philetairus socius*) over other host species, and sociable weavers are more often deceived by false alarms than the drongo's next most favored host, the pied babbler (Flower et al., 2013; Flower and Gribble, 2012). Pied babblers are cooperative group-living birds that post sentinels that alarm at approaching predators (Ridley and Raihani, 2007), and pied babblers are therefore likely to have lower intrinsic value for drongo alarm calls than sociable weavers (who do not have a sentinel system) (Ridley and Raihani, 2007). To further illustrate this point, smaller babbler groups

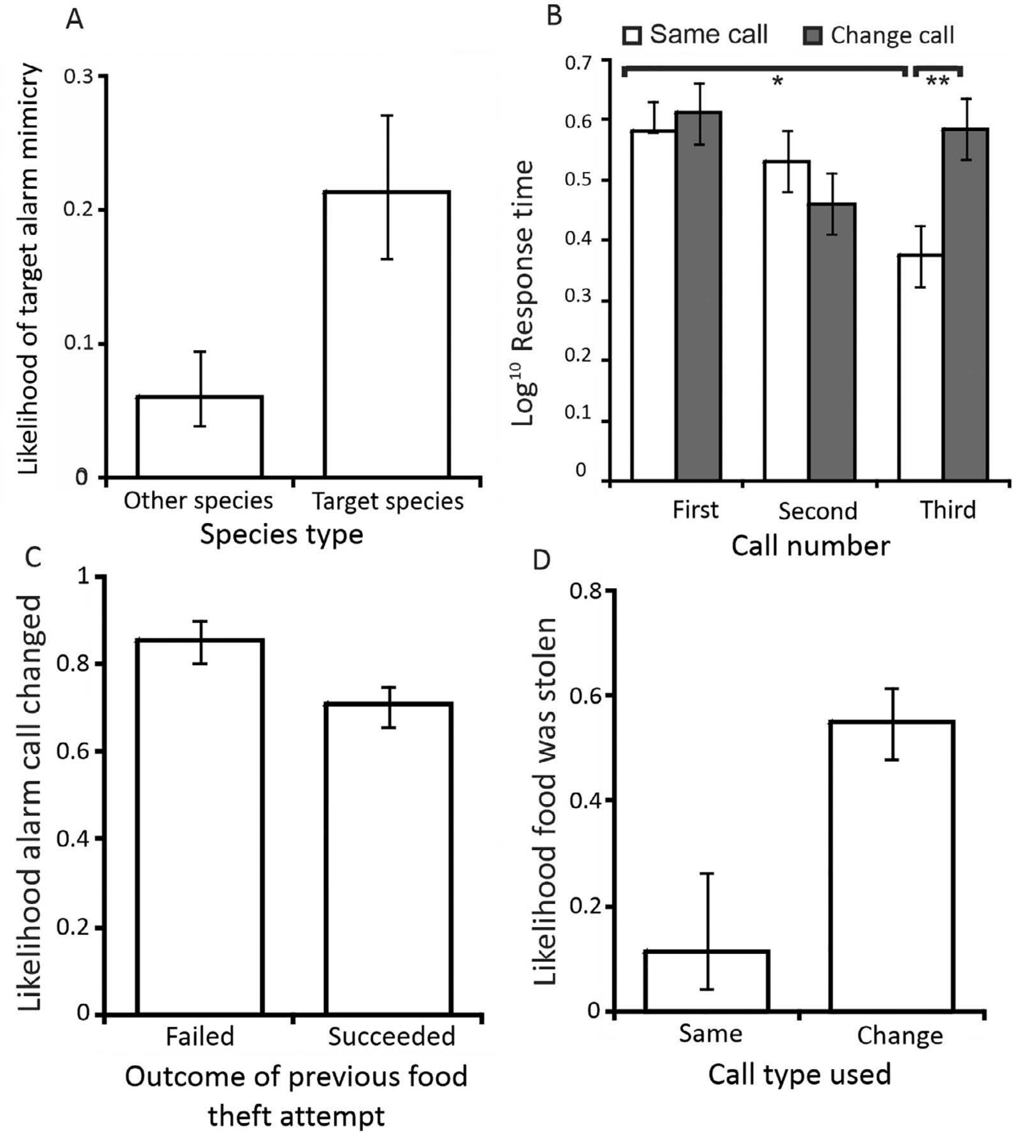

Figure 22.3 Flexible Deceptive Tactics. Drongos expand opportunities for deception by stealing food from different species and (A) preferentially mimic the alarm calls of the species they are targeting, which increases food-theft success compared to mimicry of other species (Flower et al., 2014). In addition, drongos vary calls to maintain deception; (B) alarm call playbacks revealed that pied babblers decrease their response to false alarms when the same call is made in succession, but increase their response once more when the call changes. In food theft attempts, (C) drongos typically change their false alarm type from one attempt to the next, particularly if a previous attempt failed, and (D) this increases food theft success.

have sentinels present less often, and more often respond to drongo false alarms than larger babbler groups (Ridley and Raihani, 2007). Drongos could additionally exploit contexts offering higher deception payoffs by focusing on host individuals that respond to deception more often. Indeed, drongos target younger pied babblers, which are perhaps less able to discriminate honesty and deception (Ridley and Child, 2009).

(iii) Tactical variation of true versus false alarm frequency

Tactical deception enables deceivers to moderate the production of deceptive signals such that they deceive for highest payoff, or produce honest signals to increase apparent reliability and therefore future deception (Byrne and Whiten, 1988). For example, drongos enhance their alarm call reliability, and additionally the intrinsic value of the call for their host, by alarming at terrestrial predators only when with pied babblers (a terrestrial forager vulnerable to terrestrial predators) (Ridley et al., 2007). Drongos also forego opportunities to use deception, since they often attempt to steal food through physical attacks on hosts, even though overall food-theft success is greater when they produce false alarms (Flower and Gribble, 2012). Instead, drongos preferentially use false alarm calls for scenarios where they are targeting larger host species better able to defend themselves. That drongos employ honesty when it suits their host and constrain deception to contexts of greatest value, further illustrates the potential benefits of flexibility and control for deception payoffs.

Parasitism to mutualism: tactical deception favors the evolution of cooperative behaviour

Although deceivers manipulate receivers, they may also produce cooperative behaviours that benefit receivers and facilitate future deception (Baigrie et al., 2014; Radford et al., 2011). Accordingly, when following hosts, drongos whistle a ‘watchman’s song’ that signals an absence of predators and enhances host foraging through reduced host vigilance and increased foraging efficiency (Baigrie et al., 2014; Radford et al., 2011). Sociable weavers are attracted to the drongo watchman’s song, suggesting that they gain net benefits from associating with drongos as a mutualist despite the costs of parasitism. Somewhat ironically, drongos even produce their watchman’s song immediately following deceptive alarms, which speeds-up the resumption of weaver foraging behaviour. The cooperative watchman’s song therefore increases deception payoffs, yet also raises host benefits by attracting hosts and increasing the intrinsic benefit of drongo alarms as well as the rate of host food finding. Indeed, cooperative relationships where both parties ultimately gain net benefits may be an inevitability for tactically deceptive species, and perhaps societies, to maintain and optimize deception.

Although deceivers may benefit receivers through honesty and cooperative signaling, we still expect receivers to punish deception using sanctions and physical aggression that enforce honesty, especially where relationship payoffs become negative (Raihani et al., 2012). Consistent with this prediction, pied babblers are more likely to be physically aggressive to drongos when in larger groups with more frequent babbler sentinels (Ridley et al., 2007). More generally, receivers able to recognize interactants, memorize interaction outcomes, and even generalize across an interactant’s behaviour to new contexts, would have an advantage in repeated cooperative interactions where deception is possible (Brosnan et al., 2010; Freeberg et al., 2019). Flexible deception could therefore have had important consequences for the evolution of receiver behaviour as well as that of deceivers.

Future Directions: Mechanisms of Deception

As deceptive tactics diversify in response to receiver detection of deception, we may anticipate concurrent evolution of the cognitive mechanisms governing the production of deception, as well as receiver reception, processing and perception (Brosnan et al., 2010). Deceiver-receiver coevolution may therefore have played a significant role in driving complex cognition underpinning flexible behaviour, particularly for social species where known conspecifics with different interests repeatedly interact. Research to elucidate the mechanisms of deception for free-living organisms has thus far been limited and readers should note that this area is ripe for further empirical investigation. To deduce mechanisms we rely on indirect evidence from behavioural experiments (Shettleworth, 2009; Townsend et al., 2017), or alternatively, on analysis of brain physiology where we cannot be certain that change is caused by, or correlated with, deception (Byrne and Corp, 2004). For this section on future directions, I therefore consider the proposed mechanisms of deception for deceivers, and perception by receivers, recognizing that future research has the potential to greatly expand our understanding. Finally, I focus on the possible outcome of deceiver-receiver coevolution for cognition and social intelligence, to highlight the important contribution of deception research in this area.

Deceptive behaviour production

The flexibility of deceptive behavioural tactics varies greatly between species and different cognitive mechanisms are undoubtedly responsible. Many species likely operate innate motor programs, while others employ associative learning to hone deception (Mitchell and Thompson, 1986). Indeed, associative learning is arguably adequate to account for all examples of deception observed in animals (Brosnan et al., 2010). Nevertheless, deception by some species involves persistence and variation indicative of goal-oriented behaviour which in turn requires beliefs about actions that causally obtain a desire, consistent with first-order intentionality (Dennett, 1983; Heyes and Dickinson, 1990; Mitchell and Thompson, 1986). For example, piping plover (*Charadrius melodus*) are ground nesting shorebirds which lure predators away from their nest by running away and persistently attempting to attract predator attention when the predator watches or approaches them (Ristau, 1991). If running fails to distract the predator despite persistence, piping plover change tactics and deploy a 'broken wing display' indicating they are incapable of flight and therefore more easily caught by the predator (Ristau, 1991). First-order intentionality is perhaps the most parsimonious explanation (Townsend et al., 2017), since the associative learning required for piping plover would be costly (nest loss) and result in inconsistent tactics between individuals.

Researchers have suggested that deceivers capable of tactical deception, may even have the capacity to attribute beliefs to others, termed second-order intentionality, consistent with possession of a theory of mind (TOM) (Byrne and Whiten, 1988; Cheney and Seyfarth, 1990; Dennett, 1983; Mitchell and Thompson, 1986). More broadly this idea supports the Machiavellian intelligence hypothesis (MIH) (Table 22.1) and social brain hypothesis (SBH) suggesting that TOM and increased brain size in primates and humans evolved to facilitate manipulation of others in social interactions (Byrne and Whiten, 1988; Dunbar, 1998). Although tactical deception may result from TOM in humans and perhaps other animals, the widespread assumption that it necessitates complex cognition confuses behaviour and mechanism. Tactical deception is widespread among animals (Bshary, 2002; Cheney and Seyfarth, 1990; Flower, 2011; Whiten and Byrne, 1988). For example, male topi antelope (*Damaliscus lunatus jimela*) produce honest alarm calls at predators, but also make deceptive alarm calls that decrease the likelihood females will leave the males' breeding territory (Bro-Jørgensen and Pangle, 2010). TOM is unnecessary to explain such behaviour which is functionally tactical deception, yet likely results from simple associative learning (Whiten & Byrne 1988; Jackson & Wilcox 1993; Heyes 1998; Bshary 2005). Consequently, when discussing tactical deception, one must be explicit about whether one refers to the functional behaviour, or to the cognitive mechanism responsible. Moving forward, we must design empirical studies, that exclude alternative cognitive explanations for deceptive behaviour, to better understand the cognitive consequences of selection for deceptive tactics and therefore how deception has contributed to cognitive evolution.

Receiver processing and perception

For receivers of disinformation, selection favors mechanisms that enhance perception of high-resolution sensory information to enable discrimination against dishonesty. For example, host species of cuckoos are better able to reject cuckoo eggs that are more different from their own across a variety of visual parameters, while non-host species show no discrimination (Brooke and Davies, 1988; Spottiswoode and Stevens, 2012). Furthermore, if cuckoo hosts observe more cuckoos in the environment and at their nest, they integrate this cue information on the likely frequency of deception and shift their behaviour to reject eggs more similar to their own (Thorogood and Davies, 2016). Learning also plays an important role, with stronger differentiation of deception and honesty by older individuals, those with prior exposure to deceptive signals, both personally and through observing other's responses, and those with greater familiarity with the honest signal (Aronsson and Gamberale-Stille, 2012; Davies and Welbergen, 2009; Lotem et al., 1995). Focusing on humans briefly, it has been suggested that increasing receiver discrimination drove the evolution of self-deception to better disguise cues that revealed dishonesty in communication (Von Hippel and Trivers, 2011).

In social contexts, where receivers may detect and avoid familiar deceptive individuals, we anticipate mechanisms to support reputational assessment. Reputations may be assessed through associative learning coupled to individual recognition (Brosnan et al., 2010). Representational memory of the outcome of previous interactions could further facilitate contextual discrimination (Brosnan et al., 2010; Gigord et al., 2002), leading to the possibility that organisms project representations of future outcomes contingent on current action (Boyer, 2008). Ultimately, if sufficient benefits were provided by a flexible model of when deception by different interactants was likely, selection could favor receivers able to assess intentions by representing others' beliefs, implying second-order intentionality and TOM (Byrne and Whiten, 1988). The possibility that deception may cause or contribute to the evolution of second-order intentionality in receivers has received limited attention yet illustrates how sophisticated social cognition could evolve where this enhances both deception, and the capacity to evade deception.

Social cognition

Although individually neither cooperation nor deception necessitate complex cognition, the interplay between the two could help drive cognitive evolution. Deceptive acts in social primates involve flexible signal production specific to individual interactants that may be incompletely honest, and occasionally tactically deceptive in novel contexts. For example, in one observation, a subordinate monkey about to receive aggression produced a deceptive alarm call and looked towards a fictional predator, thereby evading aggression (Whiten and Byrne, 1988). Likewise, social primates punish and sanction cheats (Riedl et al., 2012), and may use an understanding of others' intentions to guide engagement in cooperative behaviour (Cheney, 2011). Individuals can therefore play the role of both deceiver and receiver, and are hypothesized to employ cooperation tactically to better enable their deceptive acts, while simultaneously monitoring other social interactants to discriminate deceivers (Brosnan et al., 2010; Byrne and Whiten, 1988). This argument forms the basis of the MIH (Byrne and Whiten, 1988) where manipulative deception is contingent on tactically honest cooperation in other contexts. Consequently, the MIH overlaps on a broader level with the Social Intelligence Hypothesis, emphasizing interactions between individuals as central for the evolution of complex cognition and large brain size (Byrne and Whiten, 1988; Dunbar, 1998; Emery et al., 2007; Humphrey, 1976). Communication, with the inherent possibility for deception, is therefore likely to have played an important role in the evolution of complex cognition in social species with frequent and diverse interactions, including humans (Dor, 2017; Freeberg et al., 2019; Lucas et al., 2018).

A Framework for Future Investigation

Theoretical advances in recent decades have provided a framework to understand deception considering how, why and in what contexts deception occurs, and have resolved key questions about the stability of communication systems given the presence of honesty and deception (Carazo and Font, 2014; Maynard Smith and Harper, 2003; Mokkonen and Lindstedt, 2016). Additionally, research on interactions between deceivers and receivers has identified the factors affecting receiver response and the coevolutionary consequences, including the evolution of flexible deceptive tactics. However, our understanding of deception is presently hampered by a lack of empirical research on mechanisms and how these evolve in tandem with observed deceptive behaviour and receiver responses. I therefore propose the following three avenues:

We must identify (i) what cognitive mechanisms are responsible for behavioural tactics and receiver responses. This will require experimental methods that can be applied in the field and laboratory to distinguish hypothesized mechanisms responsible for flexible deceptive tactics. Additionally, to explore why cognition evolves to facilitate deception we must identify (ii) what functional benefits are provided by different deception mechanisms. To do so we may compare payoffs available from mechanisms that enhance deception, accounting for associated costs through behaviour and physiology required to support the mechanism e.g., increased brain size (Byrne and Corp, 2004). Finally, we must consider (iii) what ecological contexts favor the evolution of different deception mechanisms. This will help us identify the prior adaptations required and the ecological scenarios that may favor complex cognition (e.g., flexible signal production coupled to social group living with individuals that have incompletely overlapping interests). Resolving these three questions will clarify how the ultimate function of deceptive behaviour and the proximal mechanisms responsible evolve in tandem. Furthermore, we may provide evidence of the role deception has played in the evolution of social cognition in animal societies, including our own.

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23

EVOLUTIONARY BEHAVIOURAL ECOLOGY PERSPECTIVES ON PERSONALITY IN NON-HUMAN ANIMALS

Niels J. Dingemanse and Denis Réale

Introduction

Behavioural ecologists increasingly focus on the ecological causes and evolutionary consequences of animal personality (Réale et al., 2007; Wolf and Weissing, 2012). **Animal personality** exists when individuals show repeatable differences in behaviour across time or contexts, where an individual's **behavioural type** refers to its average behaviour (Réale et al., 2007). Not only are individuals repeatable in single behaviours (e.g. boldness), the repeatable components of functionally distinct behaviours (e.g. anti-predator behaviour, parental care) are often correlated; among-individual correlations in repeated expressed behaviours are called **behavioural syndromes** (Dingemanse and Dochtermann, 2013), and characterize many animal populations. These discoveries suggest that animals differ in behaviour like humans differ in personality. This has stimulated a true explosion of research on this topic that continues to date. Around the end of the last century, the idea that behaviour studies should focus on the behaviour expressed by the average individual and that individual variation around this mean would merely represent **noise around an adaptive mean** formed the general paradigm in behavioural ecology (Wilson, 1998). A myriad of empirical studies emerging at that time challenged this view in multiple ways. First, meta-analyses have demonstrated that, on average, 40% of the variance in animal behaviour is attributable to variation among individuals (Bell et al., 2009). A substantial two-fifths of the variation in behaviour is attributable to variation in personality. Second, meta-analyses show that the average behaviour is heritable with an average **repeatability** of 40% and an average **heritability** of 20% (Dochtermann et al., 2015). Finally, early studies of personality in wild animals implied that this variation is currently under **selection** (Dingemanse and Réale, 2005). These findings were puzzling because they implied that selection might act to remove heritable variation in personality during the process of local adaptation, so how then could this variation persist?

Here, we review two approaches that behavioural ecologists have applied while searching for the answer to two key questions: why has variation in personality evolved in the first place, and given that it evolved, what mechanisms allow alternative personality types to coexist? To address the latter question, evolutionary ecologists studying personality used the "**phenotypic selection framework**" developed previously to explain the maintenance of standing variation in relatively stable phenotypic traits, such as skull size in adult mammals. Because they focused on stable traits, those models seek to explain why an individual's phenotype is stable. A second class of explanations used "**state-dependent behaviour framework**" developed previously by behavioural ecologists to take

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up this very challenge. They considered that contrary to other traits, behaviour does typically vary considerably within a single individual due to reversible phenotypic plasticity (Snell-Rood, 2013). This awareness led to the question of why individuals are repeatable in their behaviour, and why they are not entirely plastic instead (Wolf and Weissing, 2010). Contemporary models of animal personality thus seek to explain not just why phenotypic variation in behaviour might persist, but also why individuals are repeatable.

Of course, model **assumptions** and **predictions** require testing by empiricists (Dingemanse and Wolf, 2010). Behavioural ecologists have done just that. Over the past two decades, many have evaluated how well adaptive contemporary models explain the existence of personality (e.g., Niemelä and Dingemanse, 2018; Royauté et al., 2018). In this chapter, we illustrate approaches we have taken in our research on personality in small birds (passerines) and mammals (rodents). We describe both observational and experimental studies aimed at testing whether those species have personality. We also detail which proposed adaptive mechanism explains personality in our study species.

The phenotypic selection framework

The classic **mutation-selection balance** hypothesis has been rejected as an explanation for the maintenance of variance in behaviour, as selection varies both in magnitude and direction (Penke et al., 2007). In this section, we list five (classic) explanations for why genetic variation in a trait is maintained. All require estimating both the causes of phenotypic variation in a trait and selection acting on it.

Phenotypic variation is one of the *sine qua non* conditions for selection to operate and for evolution to occur. **Phenotypic variation,** called V_P, is the trait variation measured on the organisms. For behaviour, it can be broken down into a **within-individual component** (V_W; within-individual variance) and an **among-individual component** (V_I; among-individual variance). The latter component (V_I) consists of a **permanent environmental component** (V_{PE}, which includes developmental plasticity) and an **additive genetic component** (V_A). The **animal model**, a mixed-effect model incorporating a relatedness matrix obtained from a pedigree, can partition variance into genetic and non-genetic components (Kruuk, 2004). V_A is essential for evolution, because responses to selection require non-zero heritability ($h^2= V_A/V_P$). Evolutionary biologists thus focus mostly on V_A. In the case of personality differences, researchers instead often focus on V_I: they study whether an individual's **average behaviour** affects its fitness. This focus makes sense because this is how behavioural ecologists define animal personality (Dingemanse et al., 2010), but also, for many behaviours pedigree data required for estimating V_A is simply not available.

The **phenotypic selection approach** (Lande and Arnold, 1983) is generally used to estimate the direction and shape of selection. The linear effect of a standardized trait value (z) on fitness values relative to the average population mean estimates the **standardized selection gradient**, an index of the strength of directional selection (β). Its quadratic term (z^2) estimates non-linear selection (γ), including stabilizing/disruptive selection. The interaction effect of two traits on fitness estimates selection acting on optimal traits correlations, and is called **correlational selection** (δ). We present here the full phenotypic selection model:

$$w = \alpha + \beta_1 z_1 + \beta_2 z_2 + \tfrac{1}{2}\gamma_1 z_1^2 + \tfrac{1}{2}\gamma_2 z_2^2 + \delta_{1,2} z_1 z_2 + \varepsilon_{1,2},$$

Here, α is the intercept for relative fitness (w), β_1 and β_2 the directional selection gradients, γ_1 and γ_2 the non-linear selection gradients, $\delta_{1,2}$ the correlational selection gradient, and $\varepsilon_{1,2}$ is the residual. A non-zero correlational selection gradient can indicate the presence of a **fitness ridge** indicative of an optimal combination of two traits (Figure 23.1A). Such fitness ridges may imply alternative multivariate phenotypes with equal fitness (a "flat" ridge; as in Figure 23.1A) but can imply multivariate directional selection (a "rising" ridge; as in Figure 23.1B, Phillips and Arnold, 1989). The former

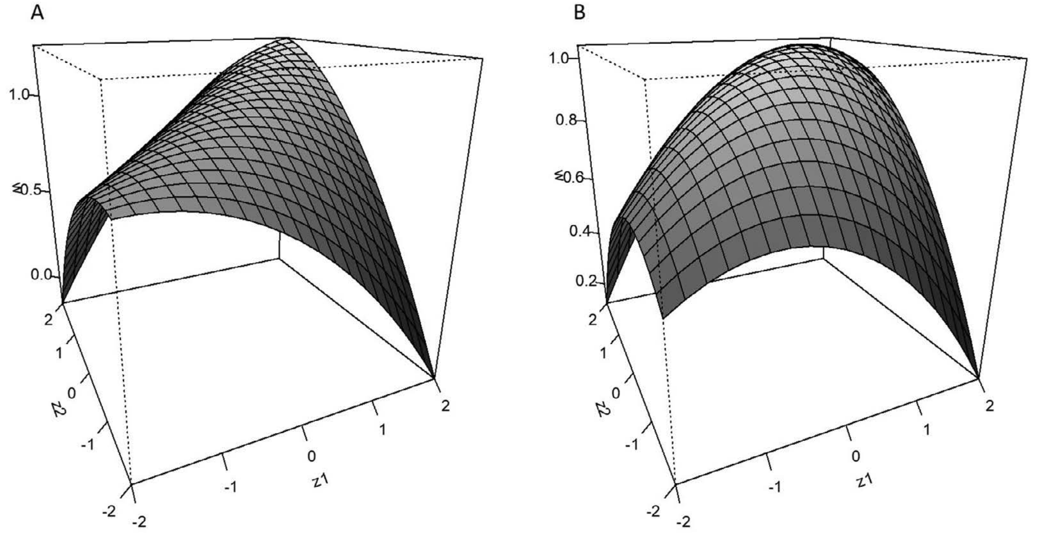

Figure 23.1 Fitness ridge caused by correlational selection between two traits (z_1 and z_2); *w* is the relative fitness of an individual. In the main text, z_1 is a behavioural trait, and z_2 can be another behavioural, life history, or morphological trait (i.e., correlational selection between two trait), a feature of the habitat used by an individual (i.e., spatially fluctuating selection), or the average value of the neighboring individuals (i.e., frequency-dependent, or social selection). (A) A correlational selection surface with a "flat" ridge drawn from equation 1 as a model, where $\alpha = 1$; $\beta_1 = \beta_2 = 0.05$; $\gamma_1 = \gamma_2 = -0.07$ and $\delta_{1,2} = 0.15$. (B) A correlational selection with a "rising" ridge ($\alpha = 1$; $\beta_1 = \beta_2 = 0.05$; $\gamma_1 = \gamma_2 = 0.07$ and $\delta_{1,2} = 0.08$). The two planes differ only in their correlational selection gradient: a decrease in the strength of $\delta_{1,2}$ (i.e., from A to B) increases the influence of non-linear selection gradients.

case is of interest to personality research, as evidence for correlational selection and flat fitness ridges may imply that alternative strategies, such as a bold-aggressive vs. a shy-subordinate phenotype may have equal fitness.

The phenotypic selection approach, however, has two main limitations. First, firm tests of selection require estimates of genetic covariance between traits and fitness (Morrissey et al., 2012). Said differently, we would expect that selection acts directly on individuals' **breeding values**, the magnitude by which the additive effects of their genes affect their phenotype for a trait, not on the variation in the trait caused by the environment. Second, researchers applying the approach normally calculate an individual's average phenotypic value based on few repeated measurements (Dingemanse et al., 2021). Many studies assume that a single measurement of an individual's phenotype is representative of an individual's average phenotype, or by extension, its breeding value. Such practices, unfortunately, lead to greatly biased estimates of selection, particularly for behaviour (Dingemanse et al., 2021). The solution is to collect repeated measures of each individual's phenotype. **Error-in-variable** models, that simultaneously estimate an individual's **predicted average phenotype** from the data as well as its effect on fitness, represent modern methods to overcome this concern. In the context of personality, it would allow one to estimate a **latent variable** that represents an individual's personality to which the phenotypic selection approach is then applied (Dingemanse et al., 2021).

There are five key classic explanations for how selection can act to maintain phenotypic variation. The first explanation, **temporally fluctuating selection**, hypothesizes that the direction of selection changes over time, so that selection cannot erode trait variance (Siepielski et al., 2009). A classic example comes from sticklebacks, where selection favors long spines in winter because animals with long spines are more likely to survive predation by birds, the main predators in winter. By contrast, selection favors short spines in summer because animals with short spines are more likely to escape predation attacks by dragonfly larvae, the main predators in summer (Reimchen and Nosil, 2002). In the context of personality, various studies have collected data on individual fitness and phenotypes for one behavioural trait (z) over several discrete periods, such as months, seasons, or years. If selection varies because the environment varies over time, so does the regression of the trait on fitness (β). This is the case in wild rodents (Boon et al., 2007), ungulates (Réale and Festa-Bianchet, 2003), birds (Dingemanse et al., 2004; Mouchet et al., 2021; Nicolaus et al., 2016), and fish (Adriaenssens and Johnsson, 2013). Of course, if we detect significant variance in selection across periods, the final step is to evaluate whether this is because selection gradients varied only in strength or also in sign. This distinction is important because only if selection fluctuates in sign, can we conclude that fluctuating selection occurred. Importantly, temporal fluctuating selection can only maintain variation in the behavioural trait if a fraction of the population is hidden from selection at any time (Sasaki and Ellner, 1997), for example, because some individuals are in dormancy, because selection acts differently on males vs. females, or young vs. old individuals.

Two scenarios can explain **spatially fluctuating selection**. In the first, individuals are distributed randomly over space. At the level of the population, there is no effect of the behavioural phenotype (z_1) on fitness. For example, in some passerine birds, there is no net selection on personality (Mouchet et al., 2021) yet personality does vary spatially (Dingemanse et al., 2012). As selection in such cases will favor local adaptation, variation within any specific site then persists because of a balance between immigration and selection. In the second scenario, animals choose to settle in a specific habitat, and habitat features can thus be considered as another trait (z_2). We thus can evaluate whether correlational selection acts to favor the correlation between z_1 and z_2, with z_2 being the chosen habitat feature. To maintain variation in z_1 the correlational selection gradient should represent a fitness ridge, i.e., there is an optimal combination of behaviour for each habitat. Individuals with different phenotypes may then perform identically in different habitats (as shown by the flat fitness ridge in Figure 23.1A). This scenario can occur with **matching habitat choice** (Edelaar et al., 2008), where individuals learn to use habitats in which they perform best. Some evidence exists for this mechanism for personality: in expanding populations of Western bluebirds *Sialia mexicana*, selection favors aggressive birds at the front of the expansion but less aggressive birds behind it. While correlational selection has not been estimated, aggressive birds are more dispersive and therefore more likely to end up in habitats where they do best (Duckworth and Badyaev, 2007).

Another key mechanism is **frequency-dependent selection**. Frequency-dependent selection can be negative, when there is a rare phenotype advantage as in the famous **rock-paper-scissors** game (Sinervo and Lively, 1996). Frequency-dependent selection can also be positive (when individuals do best when they behave the same as others). Negative frequency-dependent selection occurs if the average phenotype for a trait (z_1) negatively affected selection (β) on an individual's phenotype for another trait (z_2), while positive interaction effects imply positive frequency-dependent selection. Figure 23.1A shows positive frequency-dependent selection. This mechanism for the maintenance of variation is appealing, as it only requires interactions between individuals. Frequency-dependent selection is one way by which **social selection** (Wolf et al., 1999) can come about. With social selection, we expect that an individual's social environment (the average phenotypes of individuals interacting with the focal individual) indirectly affects the focal individual's fitness. Studies on forked fungus beetles (*Bolitotherus cornutus*) have found a positive directional selection gradient and a negative social selection gradient on male body size. Large males surrounded by small neighbors have a higher copulation success (Formica et al., 2011). In mixed colonies of lesser kestrels (*Falco naumanni*) and jackdaws (*Corvus monedula*), the activity level of both conspecifics and heterospecific neighbors affected jackdaw breeding success (Campobello et al., 2015).

The maintenance of behavioural variation can also involve a **trade-off** between current and future reproduction or survival, along the slow-fast life history continuum (Ricklefs and Wikelski, 2002).

According to the **Pace of Life Syndrome Hypothesis** (POLS) a (behavioural) trait that modulates this trade-off may have coevolved with the slow-fast continuum (Réale et al., 2010). We should thus expect a phenotypic or genetic correlation between the modulator trait and life history traits, and different combinations of these traits should affect fitness differently. For example, highly aggressive individuals with a very high early fecundity and lowly aggressive individuals with low fecundity should show the highest lifetime reproductive success. In the context of POLS, z_1 would be a focal behavioural trait and z_2 a life history trait illustrating capture variation in POL. For example, depending on the species, z_2 could represent generation time, age at first reproduction, early fecundity or longevity (Araya-Ajoy et al., 2018). The ridge of high fitness shown in Figure 23.1A then illustrates that selection would favor different personality types to make different life-history decisions that would equalize fitness across individuals.

Finally, the sexual **antagonistic selection** hypothesis posits that variation in trait z_1 is maintained because phenotypes that are favored in one sex are disfavored in the other sex: genes that are good for the former are not for the latter. For instance, in sexually dimorphic species, features that favor male survival and reproduction may not favor survival and reproduction in females. For example, male red deer (*Cervus elaphus*) with a high fitness sire daughters with a low fitness (Foerster et al., 2007). In Sable Island horses (*Equus ferus caballus*), selection favors smaller males and larger females (i.e., withers-knee length), a trait that is moderately heritable and that shows positive cross-sex genetic correlation (Regan et al., 2019). We cannot use the correlational selection framework to test the antagonistic selection hypothesis, but we can estimate selection gradients on males and females separately. When doing so, we expect a positive selection gradient β_1 in z_1 in one sex matched with a negative selection gradient in the other. The trait should also be heritable and show a positive cross-sex genetic correlation.

The state-dependent behaviour framework

Behavioural ecologists have developed a suite of formal adaptive theory explaining the evolutionary emergence of personality (reviewed by Dingemanse and Wolf, 2010). The key question is under what ecological conditions repeatable differences in behaviour, and repeatable differences in suites of correlated traits, will evolve. This question is important as animal behaviour is extremely plastic. Indeed, individuals continuously modify their behaviour in response to changes in e.g., perceived predation risk and food availability, thereby maximizing genetic fitness. Following a seminal paper by Wolf et al. (2007), a suite of adaptive models implied that personality differences can evolve in response to differences in "state", defined as characteristics of individuals that affect the net balance of costs versus benefits of behavioural actions (**state-dependent personality models**). Those models focused on understanding individual differences in "boldness" defined as behaviours facilitating resource acquisition at the cost of increased risk of mortality (e.g., predation, parasitism). For example, animals with body armour (a "state") could behave more boldly during foraging (e.g., forage in the open) because the armour mitigates the risk of predation. Meta-analyses broadly confirmed predictions of state-dependent models (Niemelä and Dingemanse, 2018). Nevertheless, initial state-dependent models were firmly criticized because they did not explain why individuals should be repeatable in state in the first place (McElreath et al., 2007). Obviously, if the optimal behaviour depends on state, and models assume "stable" states, personality differences will evolve. Follow-up models resolved this shortcoming by postulating that stochastic differences in initial state among individuals could result in stable states and stable personalities through positive feedback loops between state and behaviour (**state-behaviour feedback models**, Sih et al., 2015). Yet this idea still awaits firm experimental testing. The idea, however, is simple and appealing. Imagine that there are two prey types with equal profitability, and one individual faces one of the prey types while another individual faces the other of the prey types. Both learn from their experience and become skilled in handling their respective prey. So when given a new choice, each chooses the prey type previously encountered because this prey now has increased profitability. This is an example of a positive feedback loop that leads to repeatable differences in state and behaviour (Sih et al., 2015).

Classic and contemporary explanations for personality have many of the same ingredients. Specifically, state-dependent personality models imply that the optimal behaviour varies as a function of "state". Here, state could represent a feature of the individual, and therefore such models imply the occurrence of **correlational selection**. State can also refer to aspects of the external environment, and thus aligns with the notion of **temporal or spatial variation in selection** maintaining variation. Finally, state can refer to the social environment, such as the frequency with which a certain personality type occurs and thus aligns with the notion of **negative frequency-dependent selection**. An important problem, however, that characterizes classic explanations and state-dependent personality models alike is that either type "only" explains the maintenance of variation. They do not reveal why variation occurs among individuals. For example, selection may favor a mix of hawks and doves but classic models do not predict whether the evolutionary stable strategy is one **conditional strategy** vs. an equilibrium mix of individuals each playing a **fixed strategy** (Dall et al., 2004). The state-behaviour feedback loop mechanisms offer a key solution here as they explain why selection might favor the evolution of repeatable variation in suites of correlated traits (states and behaviours) that characterize animal personalities (Sih et al., 2015).

Insights from studies on small mammals and birds

Eastern chipmunks

Eastern chipmunks (*Tamia striatus*) are small solitary, burrow-dwelling Sciurids. In the deciduous forest of Mount Sutton, Quebec, Canada, they feed on plants and animals, but mostly on seeds of red maples (*Acer rubrum*) and American beech trees (*Fagus grandifolia*). Beech and maple seed production fluctuate between years. They synchronously produce seeds in abundance only every other year, the red maples in spring, the beeches in late summer (Bergeron et al., 2011a; Tissier et al., 2020). Massive seed production events are called "masts". Such pulsed resource dynamics affect many aspects of eastern chipmunks' ecology, including their personality.

Mount Sutton chipmunks breed yearly, but not at the same time. In mast years, they mostly consume the red maple samaras available in late spring (Tissier et al., 2020). In June, females in oestrus mate with several males (Bergeron et al., 2011b), and start their summer gestation. In September, juveniles emerge from their maternal burrows and disperse to find their own burrow, synchronized with the peak of beech seed availability (Bergeron et al., 2011a). Chipmunks reproduce again in the spring following a mast year. In late May, a new cohort of juveniles emerges from the maternal burrows. Yet the summer of that non-mast year, as well as the following spring, they do not breed again. Such a particular breeding schedule depends on the pulsed resource dynamics imposed by the dominant trees.

Because of the pulsed resources dynamics, the juveniles of the summer cohort can reproduce for the first time of their lives at seven months (i.e., early breeders). However, some individuals in this cohort escape the first breeding opportunity and must wait until 22 months (i.e., late breeders; Allain, Tissier, Garant, Bergeron and Réale, unpublished). Juveniles of the spring cohort must wait until the next breeding season, which does not arrive until 15 months later (intermediate breeders; Montiglio et al., 2014). The three groups of individuals breeding for the first time at different ages differ in their actuarial and reproductive senescence patterns. Early breeders begin to senesce and die before intermediate and late breeders, indicating the presence of a trade-off between age at first breeding and future breeding or survival (Allain J., Tissier M. L., Bergeron P., Garant D. and Réale D., pers. comm.). Chipmunks differ in risk-taking and exploration (Montiglio et al., 2010). Exploration in the open field (i.e., high positive value = fast and superficial exploration; Figure 23.2) decreases with docility (Montiglio et al., 2012), and positively predicts trapping rate and home

Figure 23.2 Exploration in eastern chipmunks is measured in the wild with an open-field test (left). Chipmunks are placed in this novel environment for 30s; after 60s in the entry tunnel (top right), their movement is recorded. After the test, they are transferred from the open-field apparatus to the site of capture.

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range size (Montiglio et al., 2012). Fast explorers have increased heart rate under restraint (Montiglio et al., 2015), suggesting high reactivity of the sympathetic nervous system and a low reactivity of the parasympathetic system, as predicted by the **coping style hypothesis** (Koolhaas et al., 2010). In summer, they also show a lower variability in fecal cortisol concentration (Montiglio et al., 2015), reflecting decreased **stress reactivity** (Koolhaas et al., 2010). Rates of vigilance decline with exploration, and fast explorers emit fewer alarm calls in risky situations (Couchoux et al., 2018). They are also more aggressive during competition for food (Couchoux et al., 2021).

Early breeders are faster explorers than intermediate ones (Montiglio et al. 2014). Furthermore, fast explorers reproduce earlier and start senescing earlier than slow explorers. Finally, selection favors fast explorers among the early breeders, but slow explorers among the intermediate breeding cohort (Montiglio et al., 2014), implying **fluctuating selection** on exploration. Average lifespan in chipmunks is around two years (Bergeron et al., 2013), and thus exploration seems to play a strong role in modulating life-history decisions. The association between exploration and the fast-slow life history continuum is one of the first examples of the existence of a **pace of life syndrome (POLS)** in a wild population (Réale et al., 2010).

A **quantitative genetics** analysis of behavioural (i.e., exploration, docility, trappability, core home range), morphological (i.e., body mass) and life-history traits (i.e., relative fecundity, sexual maturity, longevity) shows that most traits are lowly **heritable** (i.e., <0.08), but some are highly **repeatable** due to birth cohorts, permanent environmental effects and permanent social effects (Santostefano et al., 2021). Depending on whether she gives birth in the summer or the spring, a female can produce offspring that are early breeding, fast explorers, or late breeding, slow explorers. We suspect the influence of early life conditions, either directly through environmental cues perceived in or outside the natal burrow, or through the mother during gestation or lactation. Possibly, chipmunks facultatively adjust their pace of life towards a fast or a slow lifestyle depending on their predicted POLS-dependent fitness outcomes. **Social and direct selection** pressures also act on these traits (Santostefano et al., 2020). Social selection gradients estimated for female docility and male body mass imply that females with docile neighbors and males with large neighbors have lower fitness. Variation in selection gradients with the season further implies **temporally fluctuating selection**.

Great tits

One of the major models in personality research has been the great tit *Parus major*. Early studies in the mid-1990s showed that hand-raised great tits differed in suites of correlated traits, where fast (compared to slow) explorers were also bolder in approaching novel objects and more aggressive in pairwise confrontations (Verbeek et al., 1994). The two types of birds also differ in stress physiology (Groothuis and Carere, 2005). Further, **quantitative genetic** studies (including selection-line studies) showed that personality is heritable both in the laboratory (e.g. Drent et al., 2003) and in the field (e.g., Mouchet and Dingemanse, 2021). Quantitative genetic experiments, importantly, have revealed both high additive and non-additive genetic variance, which suggested that the species have been under a long history of **fluctuating selection** (van Oers et al., 2004). Molecular genetic signatures confirm this assertion (Mueller et al., 2013).

Great tits have not only become a model for understanding the genetics of **avian personality**, they have also become a model for the study of natural (and sexual) selection. This is because they readily breed in nest boxes, enabling the estimation of reproductive fitness and, because individuals can be individually marked, annual adult survival. An early study on fitness consequences of avian personalities in a Dutch population demonstrated strong fluctuating selection across years that varied in a sex-specific way (Dingemanse et al., 2004). Here, avian personality is measured with a novel environment test where wild birds are assayed in the laboratory to derive an exploration score, which ranges from "slow" to "fast" (Figure 23.3). Studies on a British (Quinn et al., 2009) and a second

Figure 23.3 Personality in great tits (*Parus major*) is assessed using a laboratory-based novel environment test from which an "exploration score" is derived.

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Dutch population (Nicolaus et al., 2016) also confirmed the notion of **temporal variation in selection** on personality, suggesting that fluctuating selection is the norm rather than the exception. Recent work estimating the sources of variation in selection across 35 study plots situated across five West-European populations has found further strong evidence for fluctuating selection (Mouchet et al., 2021). The majority of the variance in selection was attributable to macro-spatial variation in selection (differences in selection across populations: 47%), though micro-spatial variation in selection (differences in selection across study plots within populations: 13%) also played a key role. We illustrate the idea in Figure 23.4. Year-to-year variation in selection, synchronized across Europe,

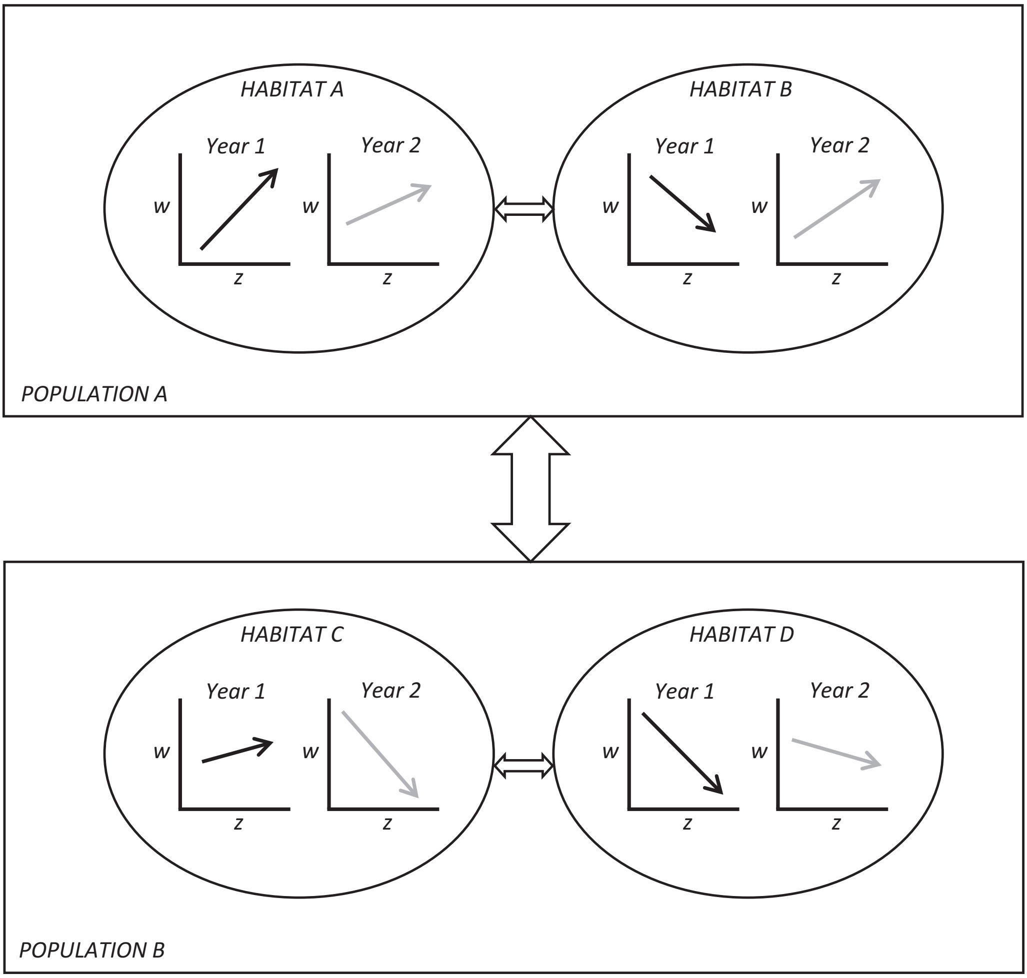

Figure 23.4 In great tits, exploration tests (Figure 23.3) were measured in many populations where fitness outcomes (survival, annual reproductive success) were also assessed. We show here a schematic overview of the variation in selection we revealed by comparing effects of standardized trait values (exploration score expressed in SD-units, *z*) on relative fitness (*w*) as detailed by Mouchet et al. (2021). The scheme illustrates two populations and two habitats within each population. It shows patterns of linear selection (arrows) for different years (black vs. gray arrows) within each habitat patch. Habitats differ in selection, as do populations (fast explorers are favored in population A but slow explorers in Population B): there is both macro-spatial (among-population) and micro-spatial (within-population) variation in selection. There is also year-to-year (temporal variation) in selection. Arrows connecting boxes (ovals: habitats; rectangular: populations) imply the occurrence of substantial dispersal mitigating local adaptation and helping preserve avian personality variation.

explained a further 19% of the variation; the remainder was attributable to population—(11%) or plot-specific temporal variation in selection (9%). This means that while spatial variation in selection would select for local adaptation, year-to-year fluctuations in selection act to mitigate microevolution and local adaptation. Moreover, great tits are greatly dispersive, with bolder, more explorative birds dispersing further (e.g., Dingemanse et al., 2003). This implies that the migration-selection balance might represent a fitting explanation for why animal personality variation persists in this system (Figure 23.4). Importantly, there is no correlational selection for the adaptive integration of personality and dispersal (e.g., van Overveld et al., 2015), suggesting that **phenotype-environment matching** mechanisms (Edelaar et al., 2008) might not have evolved.

Experimental work focusing on testing predictions and assumptions of adaptive **state-dependent personality models** has provided further clues on why individuals might have stable phenotypes. As detailed above, strong evidence for fluctuating selection can help explain why standing heritable variation might persist—not why personality types evolved in the first place. A prominent explanation is that an individual's **residual reproductive value** (RRV), or future fitness expectations, shapes its optimal level of risk-taking behaviour (Wolf et al., 2007). Individuals with great reproductive "**assets**" should be shy and protective of those assets while those without should behave more boldly to acquire them. Manipulations of brood size and population density confirmed these predictions as animals with reduced RRV became more explorative, while animals with increased RRV became less explorative (Nicolaus et al., 2012). The ability of birds to respond to treatment implied that variation in personality of non-genetic origin may also be understood from an adaptive perspective. Further, the causal link between RRV and risk-taking behaviours implies that great tit personalities may differ in optimal life-history strategy and **pace-of-life**.

Summarizing conclusion

Multiple strands of behavioural ecology study adaptive perspectives on animal personality. We distinguish for simplicity between phenotypic selection vs. state-dependent behaviour explanations but this distinction, as we show, is somewhat mute. Explanations implying the need for studying variation in selection (Figure 23.1) versus those implying the occurrence of adaptive state-dependent personality largely make the same predictions. They predict that, rather than being fixed, selection on personality varies as a function of environmental factors (fluctuating selection), other traits expressed in the same individual (POLS, correlational selection), or traits expressed by other individuals (social selection). A nagging problem is that the majority of explanations are adequate only when assuming that individuals have "fixed" behavioural types. Much work remains to be done to predict when reversible plasticity versus personality variation (whether or not genetically determined) evolves (Botero et al., 2015). Doing so will fully embrace the notion that questions about personality center not on understanding "variation" but rather why variation exists at particular (rather than other) hierarchical levels of biological organization (Westneat et al., 2015). Our worked examples of field studies on rodents and passerines sketches a promising yet incomplete picture, compatible with the notion that selection may not favor a single optimal phenotype. A major caveat, however, is the difficulty of constructing appropriate **null expectations:** how much variation in personality do we expect under adaptive and neutral evolutionary scenarios? These types of questions require answers before we can draw firm conclusions on whether animal personality variation exists despite or because of the action of selection.

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24

SOCIAL CONTEXTUAL INFLUENCES ON BEHAVIOUR

Todd M. Freeberg and Brittany A. Coppinger

From the earliest days of writing on behaviour, we have known that an individual's social context can powerfully influence that individual's behaviour. Behaviour of individuals is often affected by the absence or presence of other individuals, and by the number, types, or composition of individuals if present. Like many ideas in organismal biology, this notion goes back to Darwin (Darwin 1871, 1872), with traces found in the writings of Lamarck (Lamarck 1809 / 1984). The notion remained important in both early ethology (Tinbergen 1953) and early comparative psychology (Carpenter 1964); see Crawford (1939) for a review of the early years of study on this question. Indeed, some of the earliest experimental laboratory work in animal behaviour pointed to the importance of social settings on individual exploration and activity (Small 1900).

In this chapter, we take a proximate approach to the question of social contextual influences on behaviour. We first describe several types of social contextual influence. We then discuss a series of recent observational and experimental studies on how variation in flocks of Carolina chickadees (*Poecile carolinensis*) influences individual chickadee behaviour. We conclude with a brief section of suggested future avenues of research on social contextual influences, including those that integrate proximate and ultimate approaches.

Some major types of social contextual influence

Historically, there has been a dizzying array of terms for social contextual influences on behaviour. Sometimes the same term is used by different authors to refer to different phenomena, and sometimes two or more distinct terms are used by different authors to explain the same phenomenon (for historical detail and critical review of this terminology, see Galef (1988) and Heyes (1994)).

Local enhancement and stimulus enhancement

Individual exploration of habitat involves energy, time, and opportunity costs as well as potential costs due to uncertainty of predation (Lima & Dill 1990). Assessing successful space and resource use of others can decrease these costs for individuals. The simple presence of other individuals in an area serves as a cue – public information – to attract individuals to that area, a process known as local enhancement (Valone & Templeton 2002; Danchin *et al.* 2004). For example, recent experimental work found that German cockroaches, *Blattella germanica*, were more attracted to a location that had conspecifics feeding than they were to a location that had conspecifics separated from the same foods, indicating the particular behaviour in an area was the attractor, and not just the combination of the

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conspecific and food stimuli (Lihoreau & Rivault 2011). Once in the area of conspecifics, important producer-scrounger dynamics can emerge that can influence rates at which individuals can learn new behavioural patterns (Aplin & Morand-Ferron 2017).

A related process is stimulus enhancement, in which individuals are attracted to a particular type of area or to a specific category of stimulus due to the presence of conspecifics associated with that area or stimulus. In other words, local enhancement involves individual attraction to conspecifics and stimulus enhancement involves individual attraction to stimulus classes associated with conspecifics. For example, in bumblebees, *Bombus terrestris*, individuals able to observe live conspecifics interact with certain experimental flower colours were attracted to different flowers with those colours (stimulus enhancement), but individuals able to observe inanimate bee models on certain flowers were only attracted to those specific flowers (local enhancement: (Avarguès-Weber & Chittka 2014).

Coaction

Once an individual is drawn to an area or stimulus because of the presence of others, it may start to perform behaviour that those individuals are producing. Coaction involves individuals producing a certain behaviour at a greater rate (or performing it more intensively) in a social context where others are producing the same behaviour. Cockroaches, *Blatta orientalis*, for example, ran a simple, straight runway more rapidly when tested in pairs than when tested alone (Zajonc *et al.* 1969). Coaction is similar to social facilitation (discussed below) but requires that conspecifics are already engaged in the behaviour in question.

Social facilitation and social inhibition

Social facilitation occurs when behavioural production (in terms of rate or intensity) increases in the simple presence of others, whereas social inhibition involves behavioural production decreasing in the presence of others (Zajonc 1965; Galef 1988). Behaviour patterns showing social facilitation effects are typically those that are well-learned or dominant in the behavioural repertoire; social inhibition effects typically involve behaviour patterns that are newly learned, or relatively subordinate in the repertoire (Zajonc & Sales 1966). The above-mentioned study of cockroach runway performance also included a more difficult maze condition and a manipulation involving the visual presence or absence of an audience of conspecifics. Individuals ran the runway in less time when an audience was present (social facilitation) but ran the maze slower when an audience was present (social inhibition), compared to when individuals were tested without an audience (Zajonc *et al.* 1969).

Coordination

Individual movement is often sensitive to the movement of others in a group and can result in individuals coordinating and sometimes synchronizing their behaviour. This sensitivity can be observed in large-scale group movement like migration and dispersal and in smaller-scale movements of flocks of birds or shoals of fish, and occurs across species boundaries (Handegard *et al.* 2012; Cote *et al.* 2017; Duranton *et al.* 2019). Coordination of behaviour in groups extends beyond movement, including ingestive behaviour (Hoppitt & Laland 2008) and signaling (Greenfield et al. 2021), and is argued to be crucial to social learning processes like imitation and emulation (Coussi-Korbel & Fragaszy 1995); we discuss signaling and social learning below.

Dominance hierarchies

The behaviour of individuals in relatively stable social groups is often constrained by their position within the group's dominance hierarchy. In classic studies of chickens, *Gallus domesticus*, for example, a peck-right hierarchy was regularly observed, in which Bird A would peck Bird B lower in the hierarchy and never be pecked by Bird B, Bird B would peck Bird C and not be pecked by Bird C, and so on (Schjelderup-Ebbe 1935). In species with strong dominance hierarchies, then, agonistic behaviour and often other behavioural systems are heavily influenced by position in the hierarchy (Chase *et al.* 2002; Curley 2016; Hobson 2020). In species with weaker dominance hierarchies (more egalitarian than despotic), such behavioural constraints are weaker; these species may further experience selection for increased signaling diversity (Bouchet *et al.* 2013), a topic we address below.

Social learning: imitation, emulation, and observational conditioning

As mentioned above, once an individual has been attracted to an area where conspecifics are, there is opportunity for a myriad of learning processes to occur. Although we might consider any learning in a social context to be 'social learning', the term social learning has often carried the connotation of processes like imitation (Galef & Laland 2005; Galef 2013). Given the heightened arousal that is thought to be a physiological basis of processes like social facilitation, however, it might be more useful to employ this broader terminology of social learning as different types of learning that occur in a social setting. For example, speed and extent of individual learning (classical conditioning and operant conditioning) have long been known to vary depending upon whether the individual is tested alone or in a group (Crawford 1939).

When an individual observes another individual perform a behaviour, its subsequent behavioural production can be influenced by this experience. In some cases the observer copies the movement actions of the performer to reach the same goal as the performer, and this behavioural copying is called imitation (Galef 1988). Oftentimes the observer fails to perform the exact pattern of behaviour it observed the performer produce, but is able to reach the goal anyway – this is the process of emulation. A simple way to test these two processes against one another is to use a bidirectional control procedure, in which a performer manipulates an apparatus in a particular direction – for example, sliding a window up or down to gain a goal – and assessing whether the observer performs the action in the same direction when both directions will reveal the goal. Dogs, *Canis lupus familiaris*, for example, are often observed to emulate a human performer to reach a goal like a toy, but can imitate the behaviour of a dog performer, in such a bidirectional control task (Miller *et al.* 2009).

Observers can also rapidly develop affective responses that are similar to the responses produced by performers in the context of certain stimuli, a process called observational conditioning. Rhesus monkeys, *Macaca mulatta*, who observe a conspecific performer react with a fear response to a snake in its presence themselves often develop a fear response to the snake (Mineka & Cook 1993). The fear response stemming from this observational conditioning can in turn be transferred to other associated stimuli through classical conditioning (Cook & Mineka 1987).

Audience effects

Although "audience effect" is sometimes used synonymously with examples of social contextual effects we have described above, the term is frequently used to refer specifically to communicative events. Here, an audience effect is said to occur whenever an individual's signaling behaviour is influenced by the presence and nature of a group, including the number and type of individuals present (Coppinger *et al.* 2017; see Chapter 22). For example, relatively dominant male cichlid fish, *Astatotilapia burtoni*, produced more aggressive signals and courtship signals when they could see females and subordinate males than when they could see females and more dominant males (Desjardins *et al.* 2012). Audience effects in communication have been of interest to researchers because they suggest volitional control over signaling, though considerably more experimental work is typically needed to make this claim (Townsend *et al.* 2017; see Chapter 22). Finally, behavioural coordination is often seen in signaling interactions as well, such as in groups of insects (Greenfield *et al.* 2016), anurans

(Legett *et al.* 2019), and songbirds (Rivera-Cáceres *et al.* 2018), and may function to minimize overlapping signals and masking.

Social contextual influences on Carolina chickadee behaviour

Our lab studies flocks of Carolina chickadees, *Peocile carolinensis* (Figure 24.1a), and tufted titmice, *Baeolophus bicolor*, to test how variation in social context influences individual behaviour. Chickadees and titmice are ideal species for studies of social contextual influences since many of the species form stable flocks in the overwintering months and flock sizes vary both across and within species (Harrap & Quinn 1995). We are also interested in this group of species because many of them use a structurally complicated calling system, known as the *chick-a-dee* call in North America (Krams *et al.* 2012). We often use field experiments in which we manipulate stimuli encountered by natural flocks and aviary experiments in which we manipulate the size and social composition of flocks. Our studies are conducted in eastern Tennessee, in the ridge-and-valley region between the Cumberland Mountains and the Smoky Mountains; we are in roughly the central part of the ranges for both species.

In one of the earliest studies of social contextual influence we focused on conspecific flock size (Freeberg 2006). The study had two parts: an observational component that assessed naturally occurring flocks and an experimental component in which flock sizes were manipulated in semi-natural aviaries. In the field study, calls of individuals from 30 different flocks were recorded. Flocks were categorized as small (1–2 chickadees) or large (3 or more chickadees; Carolina chickadee flocks in eastern Tennessee are relatively small, and the flocks are not always moving together in their territories). Call complexity was assessed with two measures of uncertainty related to the diversity of note types and of ordered pairs of note types used in the calls. Calls with greater diversity of note types and ordered pairs of note types have more bits of information in them, and so hypothetically can convey a wider range of messages to flock members compared to calls with less diversity in note composition. Individuals in large flocks in the field study produced calls with more information than individuals in small flocks.

This finding on greater call complexity in larger flocks was replicated during the experimental part of this study (Freeberg 2006). Experimental flocks were captured and housed in semi-natural outdoor aviaries (Figure 24.1b; 3 m width x 6 m length x 3.5 m height). Experimental flocks either

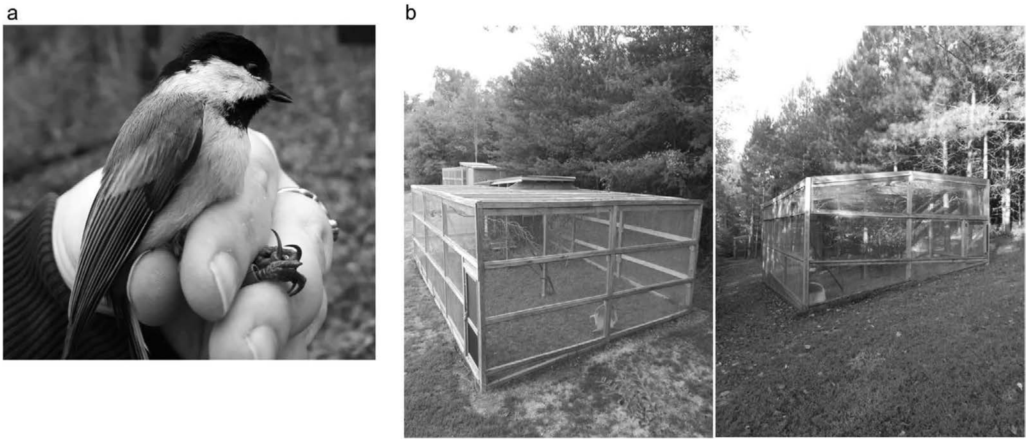

Figure 24.1 (a) Photo of Carolina chickadee (*Poecile carolinensis*); image by Brittany A. Coppinger. (b) Photos of aviaries used in experiments manipulating flock size and composition in semi-natural captive environments.

Images by Todd M. Freeberg.

contained two, four, or six chickadees. As with the field study, birds in the larger flocks produced calls with more information than birds in the smaller flocks. The combination of field and experimental work in this study demonstrated an *audience effect* – the number of individuals in a group influenced the bits of information, a proxy for complexity, conveyed in Carolina chickadee calls. Individuals in larger groups may have to produce a wider range or greater diversity of signals than individuals in smaller groups, to transmit a wider range of messages (Freeberg *et al.* 2012).

In addition to conspecific group size, our lab has investigated the effects of other aspects of variation in social context. In two studies, we assessed whether flock-mate familiarity can influence individual behaviours (Coppinger *et al.* 2018, 2019). In aviaries, we held flock size constant at four birds, and experimentally manipulated flock-mate familiarity. We did this by creating experimental flocks of chickadees caught from the same natural flock (familiar condition) and flocks in which each individual was caught from a different natural flock (unfamiliar condition). In one study, we compared familiar and unfamiliar flocks in terms of how they responded to the presentation of threatening stimuli, and in the other study we compared the two flock types in terms of their ambient (unmanipulated) behaviour.

During the observation period in the stimulus-presentation study, we exposed flocks to several stimuli that ranged in their level of threat and novelty (for example, hawk and snake models, novel plastic structures, and natural tree branches: Coppinger *et al.* 2018). We found that birds in unfamiliar flocks called later in response to these threatening stimulus presentations than did birds in familiar flocks (Figure 24.2a), revealing a potential *social inhibition* effect. Latencies to respond to non-threatening stimuli did not differ for the two flock types. Differences between birds in familiar flocks compared to birds in unfamiliar flocks even existed at the end of the experiment when birds were released individually back into their home territories. During release, birds from familiar flocks were more likely to call in flight than birds from unfamiliar flocks (Figure 24.2b).

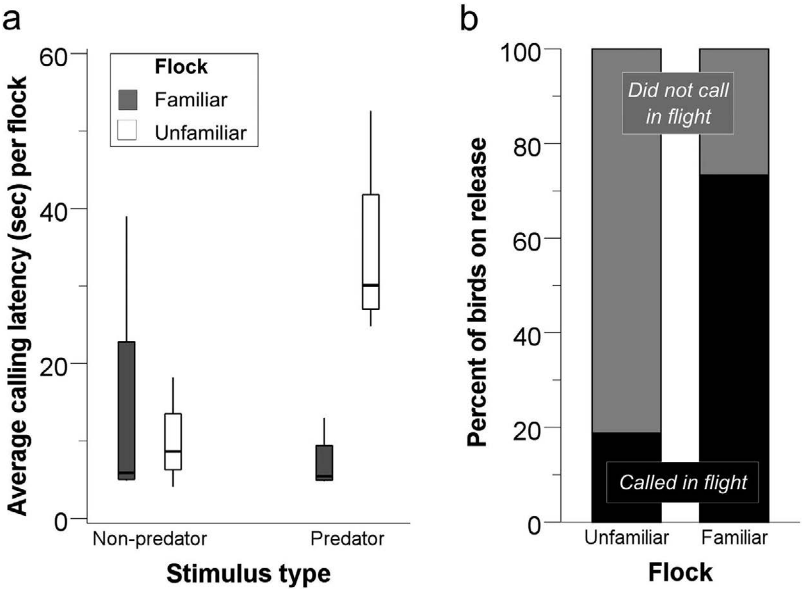

Figure 24.2 Calling responses of Carolina chickadees in 'familiar' and 'unfamiliar' flocks of four individuals. (a) Initial calling responses to predator stimuli have longer latencies in unfamiliar flocks than in familiar flocks. Data are boxplots representing medians (thick lines), 25- and 75-percentiles (boxes), and ranges (whiskers). (b) Birds from familiar flocks were more likely to call upon release at site of capture at the end of the aviary experiments.

Data adapted from Coppinger *et al.* 2018.

Additionally, we assessed the note composition and uncertainty metrics of calls produced by birds in ambient conditions with no stimulus presentations (Coppinger *et al.* 2019). Individual calling behaviour was collected from focal sample observation periods. Chickadees in familiar flocks produced calls that contained fewer introductory and hybrid D notes, but more C notes, than their unfamiliar flock counterparts. (Although we do not know the function of introductory notes and hybrid D notes, C notes are often used in calls in the context of flight: Freeberg & Mahurin 2013). However, the calls of birds in the two flock types did not differ in uncertainty metrics, nor did they differ in terms of rates of calling. Taken together, these results demonstrated another *audience effect* in that simple familiarity with one's group members influenced how individuals constructed the note composition of their calls.

Recently we have begun to investigate the role of heterospecifics as a potential social contextual influence on individual behaviour. Since Carolina chickadees often form overwinter flocks with tufted titmice, we created experimental flocks in our aviaries that ranged in the number of chickadees and titmice in each flock, using birds trapped from naturally occurring populations. We aimed to create experimental flocks in which each individual was captured from the same site and within a two-hour period to help ensure birds caught at a capture site were from the same mixed-species flocks. In this study we exposed flocks to a variety of call playbacks that varied in risk, ranging from non-mobbing *chick-a-dee* calls of chickadees and titmice to high urgency alarm calls of both species (Coppinger *et al.* 2020). Interestingly, we found that heterospecific influences were not the same for chickadees and titmice; chickadees seemed more sensitive to heterospecific presence than titmice did. Before the call playbacks, chickadees called less with more chickadees and with more titmice in the flock. The *social inhibition* of calling behaviour due to increasing titmouse and chickadee presence in this case was additive; chickadees did not decrease calling behaviour due to the relative proportion of each species in the flock. Before the call playbacks, titmice produced fewer calls with increased numbers of titmice in a flock but not with increased numbers of chickadees in a flock – suggesting heterospecific flock mate presence does not influence titmouse communicative behaviour. However, these influences changed for titmice after birds were presented with auditory stimuli. After the stimulus presentations, titmice called less with larger numbers of chickadees and larger numbers of other titmice in the flock, revealing a *social inhibition* effect on calling as described above. These results indicate that heterospecific social influences on behaviour may change in different contexts.

Although our lab mostly investigates social influences on communicative behaviour, we have also tested for heterospecific social influences on other types of behaviour, like foraging. We tested wild flocks of three target species that regularly occur in mixed-species flocks together: Carolina chickadees, tufted titmice, and white-breasted nuthatches (*Sitta carolinensis*). We exposed flocks to a novel feeder problem to determine whether social influences like flock size or mixed-species flock diversity would affect individuals' abilities to obtain food (Freeberg *et al.* 2017). We sampled from 46 different wild flocks, varying in size and species composition. We determined species diversity of flocks by using a diversity index in which the least diverse flock had a score of 1, representing a flock that had just one of those three target species present, and the most diverse flock had a score of 3, representing a flock with all three target species present and in equal proportions.

We found that flock diversity was a strong predictor of success at solving the novel feeder test in both chickadees and titmice (Figure 24.3; nuthatches rarely solved the feeder problem), suggesting a *local enhancement* effect in diverse flocks. In addition, successful chickadees (but not titmice) took seeds from the novel feeder sooner and took more seeds in total when flocks were more diverse. Flock size was not associated with success at the novel feeder test for either chickadees or titmice. Again, these results demonstrate that heterospecific presence in flocks influences behaviour of chickadees and titmice. Furthermore, social influences of group members on behaviour may be different for different species in the group, since successful chickadee flocks, but not successful titmouse flocks, were influenced by mixed-species flock diversity (Freeberg *et al.* 2017).

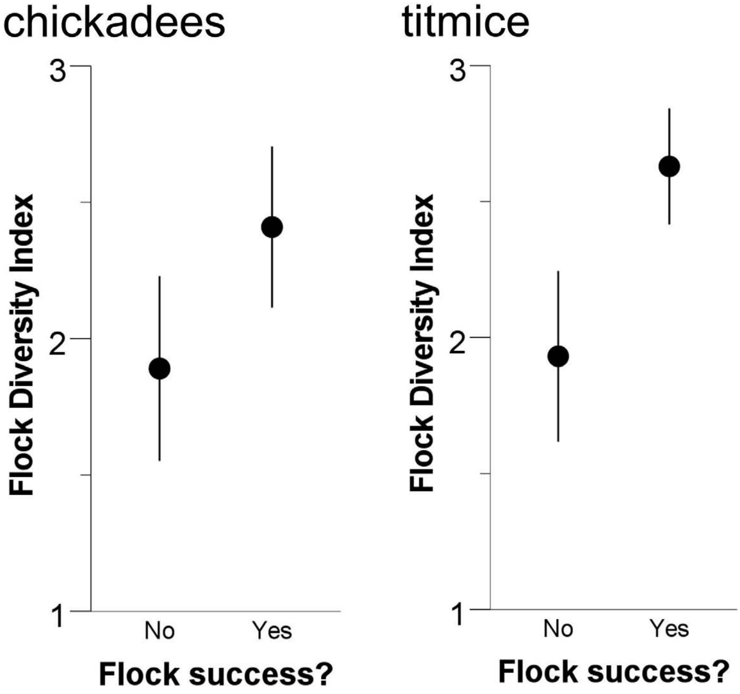

Figure 24.3 Success at a novel feeder task in wild flocks of chickadees (left panel) and titmice (right panel). For both species, successful chickadee and titmouse flocks were more diverse in terms of mixed-species flock composition than unsuccessful flocks. Data plotted are means and 95% confidence intervals.

Adapted from Freeberg *et al.* (2017).

Our above-mentioned aviary experiment that manipulated mixed-species flock sizes and compositions of chickadees and titmice also assessed these social contextual effects on behaviour other than calling, using focal sampling of individual behaviour (Coppinger *et al.* (in review)). We assessed 'close perches', in which an individual perched within 0.5 m of another chickadee for at least 2 sec, a measure of social accommodation. Our aviaries are large enough, and these flocks are small enough, that individuals could easily space out enough to avoid any close perches at all. We also assessed flight rates of individuals. Chickadees initiated more close perches in flocks with a greater number of chickadees compared to flocks with relatively few conspecifics (Figure 24.4a). Chickadees flew less in flocks with more as opposed to fewer titmice (Figure 24.4b). There were no significant heterospecific effects on rates of close perches or flying for titmice, but titmice initiated more close perches and flew less in flocks with more as opposed to fewer titmice. Thus, it appears that the asymmetrical social context effects that influence communication in chickadees and titmice also influence types of non-communicative behaviour: conspecific *coaction* or *social facilitation* for close perching and heterospecific social *inhibition* for flying for chickadees but not titmice.

Taken together, results from our naturalistic observation and experimental studies reveal important sensitivities to variation in social context in Carolina chickadees and tufted titmice. We have found social contextual influences on how *chick-a-dee* calls are constructed in terms of note composition, on rates of calling in both no- or low-risk contexts as well as high-risk contexts, on abilities to solve a novel feeder task, and on flight rates and social proximity behaviour. These birds are sensitive to variation in social contexts involving their own species. We are also starting to find that they are sensitive to variation related to the other species in their mixed-species flocks. Increased knowledge of heterospecific influences on communication and other behaviour will be fundamental for understanding the social lives of individuals in mixed-species groups (Allan 1986; Phelps *et al.* 2007; Sridhar *et al.* 2009).

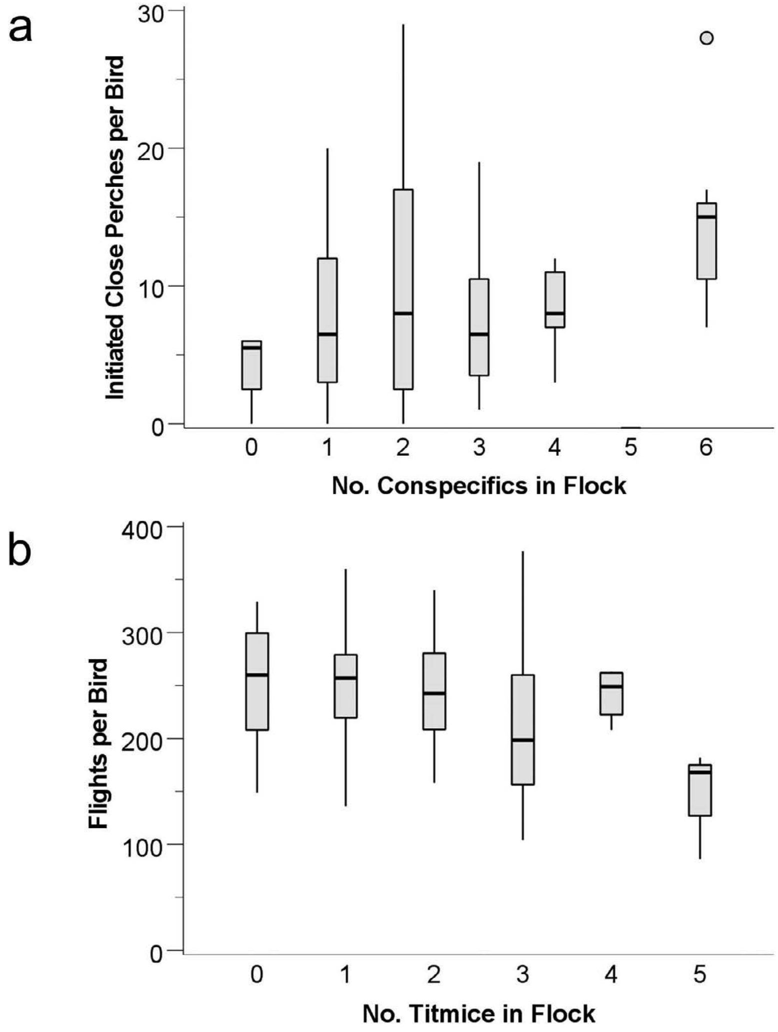

Figure 24.4 Non-vocal behaviour of Carolina chickadees in conspecific-only and in mixed-species flocks with tufted titmice in aviary settings. (a) Chickadees engage in more close perches with more chickadees in their flocks. (b) Chickadees fly less with more titmice in their flocks. Data are boxplots representing medians (thick lines), 25- and 75-percentiles (boxes), 95-percentiles (whiskers), and outliers (circles).

Adapted from Coppinger *et al.* (in revision).

Some next steps in studies of social contextual influences

Social psychology is a sub-discipline of psychology that focuses on understanding how individual thoughts, emotions, or behaviour are influenced by the presence and behaviour of others. Virtually all social psychology research today assesses only human behaviour, but this was not always so. A foundational early handbook of social psychology, for example, contained chapters on our own species, but also on insects, birds, non-primate mammals, and non-human primates, not to mention plants and bacteria (Murchison 1935). That handbook provided numerous examples of the sort of social contextual influences on behaviour that we have described here. We argue that animal behaviour research would benefit today from a deeper understanding of the history and theories of social psychology (and that social psychology would benefit from a broader analysis of individual behaviour than in just our own species).

We believe there is a need for integration of bottom-up developmental and mechanistic approaches with top-down behavioural ecological and phylogenetic approaches to gain deeper understanding of social contextual influences on behaviour (Galef & Giraldeau 2001). Given the importance of simple physical proximity of individuals to the question of social contextual influences on behaviour, let alone social learning of behaviour, a return to the study of mechanisms of orientation seems highly warranted (Fraenkel & Gunn 1961). Indeed, we know very little about the proximate and ultimate factors giving rise to the social contextual processes described here (Galef 2013). As Galef (2013, p. 127) notes, "Although for many years many laboratories have examined instances of social learning that are the result of local enhancement, social facilitation, stimulus enhancement, goal emulation, etc. . . ., such processes have rarely been treated as phenomena worthy of analysis in their own right".

An important and likely highly informative avenue of future research will be to gain greater understanding of how individuals acquire and assess social information (Danchin *et al.* 2004; Dall *et al.* 2005), and how different individuals might vary in their abilities to do so (Krause *et al.* 2010; Trompf & Brown 2014; Hobson 2020). This raises an important interface between social contextual influences and personality. It is generally held that personality drives consistent individual behavioural responses across a wide range of environmental settings, including social settings (Sih *et al.* 2004; see Chapter 23). As such, three individuals ranked high, medium, and low in boldness in one social context (like being tested alone) should show the same general rankings in boldness in another social context (like being tested in large groups). Narrow-striped mongooses, *Mungotictis decemlineata*, for example, vary in how neophobic they are, and less neophobic individuals are able to socially learn a novel feeding task quicker than more neophobic individuals (Rasolofoniaina *et al.* 2021). Diffusion of socially learned traits varies in groups of Trinidadian guppies, *Poecilia reticulata*, based upon the proportions of shy and bold individuals in the groups (Hasenjager *et al.* 2020). Such personality-like influences on behaviour can evolve extremely rapidly in some systems, and so have important ramifications for how social information is assessed and acted upon within groups (Kotrschal *et al.* 2020; see Chapter 23). Conversely, the specific social contexts that constrain behaviour in populations can likewise lead to selection for different personality types in those populations (Bergmuller & Taborsky 2010).

Species vary in terms of their levels of sociality (Krause & Ruxton 2002). This variation should relate to how sensitive individuals of different species are to social context. What types of social contextual influences are particularly important to individuals that spend much of their lives in complex social groups with fission-fusion dynamics, compared to individuals that spend much of their lives in small stable social groups, or alone? Archerfish, *Toxotes chatareus*, for example, are largely solitary, and individuals vary in how quickly they can learn to shoot a novel stimulus to obtain a food reinforcer, but this learning does not seem to depend on the social context in which individuals are tested (Jones *et al.* 2021). Conversely, the behaviour of individuals of the largely solitary octopus, *Octopus vulgaris*, is heavily influenced by the behaviour they observe a conspecific to engage in to obtain prey (Fiorito & Scotto, 1992). Clearly more work is warranted on population- and species-level variation in sociality and how this variation predicts the extent to which individuals are influenced by social context.

Important social contextual variables influencing individual behaviour include the density of individuals and variation of different personalities or behavioural types of individuals within groups or populations. These can be key proximate influence on behaviour as we have focused on in this chapter, but can also be powerful selective pressures shaping behaviour patterns in populations over generations. For example, winter survival in more social common lizards, *Lacerta vivipara*, was lower than for relatively asocial lizards in low density environments, whereas the reverse was true in high density environments (Cote *et al.* 2008). Importantly, however, more social females had higher reproductive success than relatively asocial females in both densities. Fast-exploring male junglefowl, *Gallus gallus*, obtain more matings with females than slow-exploring males in female-biased populations, but this effect diminishes with higher proportions of fast-exploring males in the local population (Roth *et al.*

2021). Fast-exploring great tits, *Parus major*, had higher likelihood of survival than slow-exploring tits in low densities, but the reverse was true in high densities (Nicolaus *et al.* 2016). These are just a few examples of studies integrating assessments of variation in personality with variation in social contextual factors, to increase our understanding of behavioural variation across populations and across generations (Wright *et al.* 2019).

As a final consideration, we know that groups vary considerably in complexity across and sometimes within species. Social complexity relates to the diversity of types of individual in a group, to variation within types of individuals, and to the diversity of connections, interactions, or relationships among those individuals (Freeberg *et al.* 2012; Bergman & Beehner 2015). How do different individuals within groups experience the diversity of possible connections to other members of their group, and how does this shape how they communicate with one another and their sensitivity to social contexts (Aureli & Schino 2019; see Chapter 25)? Studies of social networks in common chimpanzees, *Pan troglodytes*, for example, indicate that individuals in networks with a larger number of close relationships used a wider range of vocal and gestural signals than individuals with relatively few close relationships (Roberts & Roberts 2016). Because signals and cues are the primary ways in which individuals influence the behaviour of others (see Chapter 12), our understanding of social contextual influences and, more broadly, social cognition, would be strengthened by greater emphasis on the communicative interactions of individuals (Freeberg *et al.* 2019; see Chapter 17).

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25

NETWORK APPROACHES TO UNDERSTANDING SOCIAL ORGANIZATION AND COMPLEXITY

Elizabeth A. Hobson and Gerald G. Carter

Animals order their social lives in many different ways. At minimum, animals interact with conspecifics to mate and compete, but some species are consistently social and live in groups. Social groupings can be driven by ecological factors like predation pressure or available habitat, but social interactions within groups can also shape individual health, success, survival, and reproduction. As individuals interact with group members in consistent ways, social structure emerges. For individuals living within societies, these consistent repeating interactions provide guidance for how to interact with group members. Over evolutionary time, a predictable social environment may select for fixed social traits or for the ability to make flexible decisions using rules that vary from simple heuristics to complex conditional strategies. The evolution of social traits and strategies then creates new social environments. This feedback loop results in social systems that reflect selection pressures from interactions between species-specific traits (such as life history trade-offs), ecological pressures, and the social environment (Cantor et al. 2021).

Understanding how and why some animals have evolved more complex social systems than others has been a longstanding goal for the field of animal behaviour (Hinde 1976). Within the last 30 years, major advances in quantifying animal social systems have resulted from perspectives and tools from network analysis. To better understand how social structures influence individuals and vice versa (Hobson et al. 2019; Cantor et al. 2021), researchers increasingly use social networks to model the social worlds of animals in ways that are more realistic than previous models and that can be analyzed with a rich array of computational tools. This network approach typically involves building up models of the social system from interactions or associations among individuals, where each individual is represented as a 'node' and the interactions or association rates are represented as 'edges' that connect nodes (Figure 25.1). Social networks describe variation in pairwise relationships across the whole group. Networks also depict each individual's placement within the social landscape, which might convey their social connectedness, rank, power, or influence. At a larger social scale, networks can quantify connections within and among communities. At the largest scale, network structures can be summarized into a statistic describing the overall social patterns for the sampled population, which can be compared across groups or through time to document social dynamics.

Simply building a social network usually does not provide immediate insight into animal social systems (for example, Figure 25.1). As the initial excitement about creating and describing social networks wore off, researchers turned to deeper questions: Why and how do individuals form preferred relationships? What are the general structural rules that predict how individuals will interact with others? How does the individual's place in the social network influence its health, survival, and reproduction? How do individual strategies influence the structure of the network? For example,

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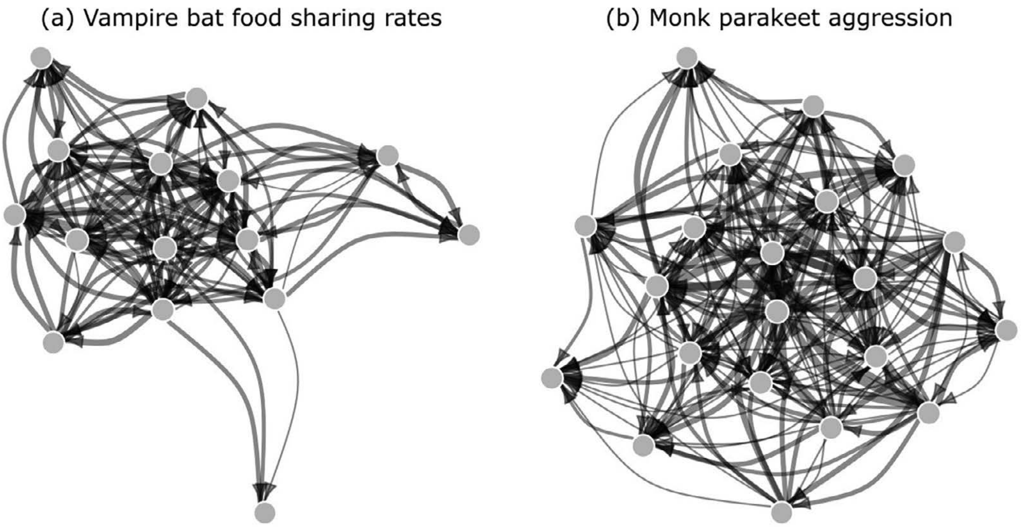

Figure 25.1 **Social networks of cooperation in vampire bats and conflict in monk parakeets.** In both networks, each individual bat or parakeet is represented by the grey circles (nodes). Both networks show directed interactions, where the origin of the arrow shows the food donor (bats) or the aggressive actor (parakeets), and the end of the arrow shows which individual received the food (bats) or the aggression (parakeets). Lines connecting individuals (edges) show whether two individuals were observed interacting and if so, how often they interacted. Thicker edges show greater mean duration rates of food sharing for the bats and more frequent aggressive events for the parakeets.

do individuals seek out particular kinds of associates such as kin or others that have similar traits to them? Do they interact based on proximity or inherit new social ties from their current associates? To address these questions, we need studies that focus on particular species as well as comparative studies applying standard methods across multiple species. Explaining why some species evolved to have more complex social structures than others can provide important insight into the evolutionary and ecological links between social structure and cognition.

We, the authors, view social complexity using the complementary lenses that focus on cooperation (Carter Lab) and conflict (Hobson Lab). In this chapter, we use the themes of cooperation and conflict to illustrate how individual behaviours, pairwise relationships, and group dynamics can lead to the emergence of different structural features.

Connections between cooperation & conflict

Cooperation and conflict are often thought of as fundamentally opposed types of social behaviours, but they are inherently linked. Cooperative societies require the evolution of individual cooperative traits that evolve in response to the frequency of exploitative free-riding or cheating – a subtle form of conflict. Similarly, dominance hierarchies emerge from individual conflict strategies that reduce mutual harm to both parties – a subtle form of cooperation. Early work described cooperation and conflict through simple “games” played once or repeatedly, often by a pair of individuals, with each individual making a single binary decision about how to act (Maynard Smith 1974; Smith and Parker 1976; Axelrod and Hamilton 1981). Each game describes a degree of inherent cooperation and conflict (Figure 25.2).

Although game theory is a useful framework for understanding the stability of different strategies over evolutionary or ecological time, most games involve simplistic assumptions (*e.g.,* two individuals each making the same kind of binary decision simultaneously, Figure 25.2). In the real world, individuals might interact repeatedly and preferentially with multiple individuals and make decisions

	partner helps	partner harms
help	OK	Worst
harm	**Best**	**Good**

Maximal conflict: best action is always to harm.

	partner helps	partner harms
help	Good	Worst
harm	**Best**	**OK**

A prisoner's dilemma: best action is always to harm, but mutual help is better than mutual harm.

	partner helps	partner harms
help	Good	**OK**
harm	**Best**	Worst

Hawk-dove game (or snowdrift game): best action depends on the partner's action.

	partner helps	partner harms
help	**Best**	**Good**
harm	Ok	Worst

Minimal conflict. Best action is always to help.

Figure 25.2 **Cooperation and conflict shown as game-theoretic payoff matrices**. Rows show possible actions of a focal actor. Columns show possible actions of a "partner" (or opponent). The relative outcomes (from best to worst) for the actor depend on the combination of actor and partner actions. Note that "help" could mean reducing aggression and "harm" could mean not helping. A rational actor would compare the best outcomes within each column to decide on an action (bold).

that can vary continuously and can depend on third-party relationships. Modeling these factors places the research into network territory. In the next sections, we review the role of social networks in understanding cooperation and conflict, with a particular focus on how our own work builds on existing foundations.

Social organization and complexity in the context of cooperation

Social evolution theory addresses the question of how cooperative traits emerge and persist when non-cooperative 'cheats' can exploit the public good of others' cooperation. This question has been a longstanding puzzle in evolutionary biology, but more than six decades of theory and evidence have now described a variety of non-mutually-exclusive solutions (*e.g.,* West et al. 2007) . Although kinship and other forms of fitness interdependence reduce the need for enforcing cooperation, many cooperative relationships and societies are stabilized in part by enforcement through partner choice, switching, reward, or punishment (Ågren et al. 2019). For example, workers in many eusocial insect societies enforce cooperation by punishing workers that attempt to lay their own eggs (Wenseleers and Ratnieks 2006).

In other societies, individuals can often choose or switch between multiple partners in a broader market of partners that might vary in their supply and their demand, which can lead to asymmetries in helping and competitive outbidding between the individuals being chosen (Noë and Hammerstein 1994). For example, when experimenters gave special food access to a single wild vervet monkey, that individual received more grooming from others (Fruteau et al. 2009). Market effects also mean that individuals that are more socially connected might have different cooperation strategies than those with fewer or weaker relationships. In societies with complex, individualized relationships (perhaps best described in primates), decisions about who and when to help can be predicted by multiple interacting social factors including kinship, similarity, social rank, past long-term familiarity, the immediate short-term costs and benefits, as well as the alternative options for partners. In sum, decisions to help can be driven by the traits of actors and receivers, their emergent relationships, as well as other relationships and the broader social network. A major challenge is therefore to better understand the relative importance of these different factors that may additively or interactively drive cooperation decisions in different species.

Social networks and cooperation

Social network structure shapes many of the key factors that influence the emergence of cooperative behaviour over evolutionary or ecological time. The rate of repeated interactions among individuals (what a social network typically describes) is a fundamental driver of cooperation (Axelrod and Hamilton 1981), because the more often two individuals interact, the greater the opportunity for mutual benefit, and the more information that can be gained about the relative quality of the social partner. Social network analysis can help researchers to identify preferred relationships and understand how they change over time (Pinter-Wollman et al. 2014). For instance, social networks of cooperation can be used to distinguish whether kin-biased helping occurs because limited dispersal leads to family groups, as in many cooperative breeders, or due to individualized nepotistic relationships, as in baboons, dolphins, and vampire bats (Lukas and Clutton-Brock 2018). In both these types of societies, the benefits of helping kin can be partially or even completely canceled by competition between kin (West et al. 2002), which depends on the scale of competition (*e.g.*, between or within groups). This scale of competition can also be illuminated by social networks (Fisher and McAdam 2017; McDonald and Hobson 2018; Montiglio et al. 2020). In sum, social networks allow the social environments to be represented in a more complex way than as separate homogenous groups.

Vampire bats as a case study

A remaining question in understanding cooperation between animals is how new cooperative relationships develop. To address this, the neotropical blood-feeding common vampire bat (*Desmodus rotundus*) is an ideal model system, because they are small, spend most of their time in tight enclosed spaces easily simulated in captivity, and form social bonds that involve cooperative behaviours such as clustering, social grooming, co-feeding, and most notably, regurgitation of ingested blood to bats that are in dire need. These different behaviours occur among both kin and nonkin, vary in cost, and can be monitored, measured, and manipulated over prolonged periods. Food donations have clear fitness benefits for the receiver because vampire bats can starve to death after missing three nightly meals of blood (Wilkinson 1984), but can otherwise survive 30 years in captivity and 17 years in the wild (Hermanson and Carter 2020). But why do vampire bats donate food to nonkin?

To understand the potential functions of food sharing, one must first consider vampire bat social structure (Wilkinson 1985a). Mean kinship in a colony is low, because all males disperse after their first year, the most dominant male cannot monopolize most paternities, and about every two years, the most dominant male changes, and a new adult female joins the community (Wilkinson 1985b). Consequently, social networks typically include mostly nonkin pairs, as well as several female matrilines with half-sisters. Although males compete for territories, females do not show reproductive competition or seasonality in most regions (Wilkinson 1985b). Individual females often move almost daily between roosts (*e.g.,* a hollow tree or cave) or between locations within a roost, yet they show clear preferred social associations over days or years (Wilkinson 1985a; Ripperger et al. 2019). These stable social bonds involve clustering, mutual grooming, and reciprocal food sharing, and are maintained when groups are moved from the wild to captivity and back (Wilkinson 1984; Ripperger et al. 2019). The bats recognize and maintain contact with preferred associates using individually variable calls (Carter and Wilkinson 2016).

The existence of these enduring female social bonds is likely why reciprocal food sharing occurs mostly among females and correlates with kinship, close association, and reciprocal grooming (Wilkinson 1984; Carter and Wilkinson 2013a; Carter and Wilkinson 2013b; Carter et al. 2019; Carter et al. 2020). Compared to males, females also have higher kinship with each other, and greater energetic needs (*e.g.,* possibly the largest investment in maternal care among bats, Hermanson and Carter 2020). Food sharing probably evolved initially through parental care and kin selection. Mothers regurgitate food to offspring, both sons and daughters feed their mothers if she is experimentally fasted (Carter and Wilkinson 2013a; Carter and Wilkinson 2015), and food donations also occur among other close kin (Wilkinson 1984). However, several lines of evidence suggest that food donations also provide donors with reciprocal direct fitness benefits, and that sharing is probably extended to adult nonkin to create a larger pool of sharing partners (Carter, Farine, et al. 2017).

Nonkin food sharing cannot be easily explained as a non-adaptive byproduct of kin selection for several reasons (Carter and Wilkinson 2013b; Carter et al. 2020). Food-sharing networks are more symmetrical than expected by chance when controlling for kinship (Carter and Wilkinson 2013a; Carter et al. 2020). Bats are attracted to contact calls from nonkin food donors but not from related non-donors (Carter and Wilkinson 2016). Nonkin donations cannot be explained by harassment because donors initiate most donations (Carter and Wilkinson 2013a) and will regurgitate food across cage bars to trapped nonkin (Carter, Wilkinson, et al. 2017).

The best line of evidence that food sharing provides direct fitness benefits comes from inspecting how new food-sharing relationships form among nonkin (Carter et al. 2020). Isolated pairs of two female strangers begin grooming and sharing food faster than females in a mixed group where one stranger meets three groupmates, or when females can freely interact with either familiar or unfamiliar females. This shows that females are not simply sharing with phenotypically similar individuals. If food sharing is a costly cooperative investment, then unfamiliar females are predicted to first use low-cost investments like grooming to 'test the waters' or 'raise the stakes' with new partners before making higher-cost investments of food (Roberts and Sherratt 1998). Unlike food donations, grooming is low-cost and can be immediately reciprocated. As predicted, the reciprocal emergence of new food-sharing relationships is predicted and preceded by mutually escalating reciprocal grooming relationships that increase before but not after sharing begins (Carter et al. 2020).

Additional evidence that food donations are reciprocal cooperative investments comes from experiments manipulating food-sharing networks (Carter, Farine, et al. 2017). According to the "social bet-hedging" hypothesis, a female bat cannot control the number of maternal relatives in her group, but she can control the number of nonkin that she feeds, so females that feed nonkin can expand their social support networks beyond the limited number of maternal kin. Even if the highest per capita inclusive fitness returns come from feeding only one's mother or daughter, this single kin partner might be missing when one is in need, so females should not put all their social investment 'eggs' in one partner 'basket'. As predicted by social bet-hedging, when we temporarily removed each female bat's primary donor, the females that had fed more nonkin in previous years coped better with the loss and received more food, but during the control condition when we temporarily removed a non-donor, the females that fed more nonkin did *not* gain more food (Carter, Wilkinson, et al. 2017). This result supports the social bet-hedging idea that as the social environment becomes less stable, it becomes increasingly profitable to invest more in relationship quantity rather than in relationship quality.

The key missing experiment to test reciprocity is to determine whether bats avoid or switch partners that do not reciprocate. If so, does the response to nonreciprocation differ between nonkin and kin? Many other questions remain. Can cooperative relationships be explained by the general cooperativeness of the actor and receiver, or are they an emergent property of that pair's unique interaction history? Does a bat's network centrality or condition affect its motivation to establish new relationships? We hope to answer some of these questions in the next few years.

Social organization and complexity in the context of conflict

Animals gain many benefits from socializing, but when animals congregate in social groups, they also often compete with group members for access to limited resources (Landau 1951a; Holekamp and Strauss 2016; Reichert and Quinn 2017). Competition can lead to conflict and aggression. In many species, this aggression is structured, leading to predictable pairwise interactions and the emergence of group-level dominance hierarchies. Ideas about dominance were first formalized as "peck order" in chickens (Schjelderup-Ebbe 1922). We now know that aggression among individuals that leads to the emergence of a group dominance hierarchy is a common structural feature for social groups across a wide range of phylogenetic space (Shizuka and McDonald 2015). Many studies show that rank also matters to individuals: higher-ranked individuals may benefit from improved health or access to resources, more reproductive opportunities, more offspring, or greater longevity (*e.g.*, Sapolsky 2005; Archie et al. 2012; MacCormick et al. 2012).

Two major perspectives have emerged in thinking about how animals achieve rank or assort themselves into hierarchies. The first focuses on the intrinsic characteristics of individuals which make them more or less likely to win a conflict, such as Resource Holding Potential (RHP, Parker 1974), where individuals interact with others to discover how willing their potential targets might be to escalate aggression or overtake their resources. Game theory has been used to model behaviours, while empirical research often used sequential round-robin contests and measures of individual characteristics to study how individuals assess each other and make decisions about aggression (Maynard Smith 1974). The second major perspective focuses on the outcomes of the conflict itself, and how individual behaviour can be modified by the outcomes of their own fights or by observing the outcomes of fights between others. For example, winning or losing a fight can change an individual's probability of success in future fights (Landau 1951b; Dugatkin 1997; Vries 1998; Rutte et al. 2006). More broadly, audience effects (*e.g.,* Zuberbühler 2008; Coppinger et al. 2017) or third-party observation of fights can also affect how individuals behave, especially in influencing which individuals they target with aggression.

Social networks and conflict

Like theoretical studies of nonkin cooperation, early work on conflict focused on pairwise interactions between individuals. Unlike much early cooperation work, however, work on conflict has more often been studied within a broader social context. For example, even in early studies, "who" each individual won fights against was important in calculating rank, not just the total number of wins. Because of this, hierarchy research has had network-like methods integrated into their main approaches before networks became a popular perspective more broadly in animal behaviour. For example, a very common method for summarizing dominance interaction data even in early papers was a table showing the wins or aggression among all pairs of animals in the group. In modern terms, this is often referred to as an interaction matrix, a common form of data used in network analyses. Because these tables were a popular way of reporting aggression patterns within dominance hierarchy papers, animal conflict is unusual among behaviour types in that researchers can more easily access data, even from much earlier studies that predate the recent push towards open science.

One of the big unanswered questions in understanding conflict between animals is the extent to which members of different species have information about their own ranks and the ranks of others in their groups, and whether animals can use this information when making decisions about aggression. The more animals "know" about their own ranks and the ranks of others, or the history of aggressive outcomes, the more they could maximize their potential gains from aggression and minimize potential losses or injury. This kind of *social information* (information about an individual's interactions, relationships, or status, held by that individual about itself or others in its group, Hobson et al. 2021a) is increasingly recognized as an important component for understanding the structure and complexity of animal societies (*e.g.*, Seyfarth and Cheney 2015; Hobson et al. 2019; Hobson 2020). This is particularly true for social systems in which the actions of the individuals (such as which individuals fight) are entwined with macro-level structural information about rank in social groups.

Testing the kinds of social information animals may have about each other is tricky. Experimentally, animals can be tested on how much information they have about rank in systems where the apparent outcome of aggression can be manipulated, causing the fight to appear or sound like it was won by the individual that actually lost (Cheney et al. 1995). Researchers using this approach can reverse apparent outcomes in ways that violate expectations if animals "know" which individual is most likely to win the fight. When played the sounds of an artificially reversed fight, uninvolved observers are often more attentive to the manipulated stimulus than to the control stimulus (where the fight outcome is consistent with expectations). These kinds of experiments have led to foundational insight into the extent of rank information in some animal groups (Cheney et al. 1995; Bergman et al. 2003). However, these experiments are very time intensive and only work when the apparent outcomes can be feasibly manipulated, making them difficult to apply across many species. An alternative approach is to gain insights into cognition from analysis of the network data using computational approaches.

Parakeets & computational approaches as a case study

Much of the research in the Hobson Lab focuses on social information: what animals know about their social worlds, how they come to know it, and what they do with that information. In the context of aggression, this focus on social information can help us better understand the open question about information in animal conflict: how much of the behaviour and decision-making that happens during aggressive interactions is based on what the animals "know" about each other? Using a combination of behavioural observations, experimental manipulations, and computational methods to determine how individuals and groups incorporate different kinds of social information has allowed us insight into the social complexity of conflict in animal groups.

Social information in conflict is particularly well-suited to these questions, because structured conflict is taxonomically widespread, biologically relevant to individuals within social groups, and strikingly similar in basic structure even across very different species (Shizuka and McDonald 2015). This surface-level similarity makes conflict networks and hierarchies one of the most promising avenues for comparative analyses of socio-cognitive trait evolution across a range of species and social systems. Within-group aggression constructs and maintains dominance hierarchies but the dominance hierarchy itself can then also play a critical role in conflict (Hobson and DeDeo 2015; Hobson et al. 2019; Hobson 2020). Hierarchies contain information about the extent to which rank can explain the ways in which individuals direct that aggression. Because of this connection between rank and behaviour, dominance hierarchy structure can serve as a critical link between social and cognitive features underlying behavioural decisions.

Much of the work in the Hobson Lab has focused on these concepts, with research that started in an empirical context with studies of aggression and rank in monk parakeets (*Myiopsitta monachus*). The parakeets are native to temperate South America and share many social features with vampire bats. They are highly social, aggregate in colonies, and can share communal nest structures that they use year-round as roost sites (Eberhard 1998). In the wild, flocks of monk parakeets have high fission-fusion dynamics where the size and composition of flocks change frequently (Hobson et al. 2014). The parakeets have individually recognizable calls that, in contrast to many parrots, encode more individual information than markers of social group affiliation or geographic origin (Smith-Vidaurre et al. 2020), which enables them to identify each other by call and preferentially associate with particular group members (Hobson et al. 2015).

In semi-naturally housed captive groups, monk parakeets quickly form consistent dyadic aggressive relationships and structured dominance hierarchies (Hobson et al. 2013; Hobson et al. 2014; van der Marel et al. 2020). After first documenting that hierarchies formed in parakeet groups, a collaboration with Simon DeDeo, a complex systems social scientist, allowed us to approach the monk parakeet aggression and rank data from a computational angle. Our initial work with the parakeets showed that their hierarchies can become structured above and beyond the simple structuring for a basic dominance hierarchy, and patterns of aggression in newly formed groups rapidly transitioned from unordered to structured. Our new computational methods showed that individuals shifted to preferentially aggressing against targets ranked slightly below their own rank in the hierarchy (Hobson and DeDeo 2015). We found that the course of conflict was shaped by how individuals synthesized social information and how they strategically leveraged this information in their decisions about aggression.

Our follow-up work expanded on these computational methods to consider how groups might structure their aggression in other species, in collaboration with Dan Mønster, a behavioural economist with a background in physics. By combining our perspectives, ideas, and skills, we developed a new social assay for aggression applicable to any group (Hobson et al. 2021a). This analysis allowed us to detect and categorize the general social dominance pattern used by the majority of individuals in the group. We described three main patterns: the *downward heuristic*, where groups follow the basic rules of a hierarchy (attack individuals ranked below self), *close competitors* (preferentially attack individuals ranked close below self), and *bullying* (preferentially attack individuals ranked far below self).

With a large historical dataset of dominance in 85 species (Shizuka and McDonald 2015), we examined whether rank information was present and in use in each of 172 independent social groups. Many groups fought using basic dominance hierarchy rules (downward heuristic) while some used multi-faceted patterns such as attacking close competitors or bullying bottom-ranked animals. None of these social dominance patterns were phylogenetically restricted to particular orders, providing evidence that similar levels of social information could emerge in species despite potentially large differences in their cognitive abilities (Hobson et al. 2021a). This work also shows that groups of the same species can exhibit different dominance patterns, and therefore social dominance patterns in a population should not be generalized to the entire species.

Future advances and conclusions

Modeling social dynamics to draw inferences about cooperation and conflict requires high-quality data. Fortunately, recent technological improvements in biologging developed by interdisciplinary teams of biologists, engineers, and computer scientists, can now provide data of unprecedented spatial and temporal resolution (Ripperger, Carter, et al. 2020; Smith and Pinter-Wollman 2021). The big datasets from these systems enable computational and statistical approaches for understanding changes over time (Pinter-Wollman et al. 2014), integrating multiple layers of social information (Silk et al. 2018; Finn et al. 2019), and facilitating the experimental manipulation of social networks. For example, proximity loggers allow us to track how vampire bat social networks change as individuals are released from the lab to the wild or as individuals get sick and recover (Ripperger et al. 2019; Ripperger, Stockmaier, et al. 2020). Combining big data from empirical studies with computational tools and social network analyses can allow researchers to tackle some of the big outstanding questions about animal sociality and to study the emergence of social structure from variation in individual traits to relationships and groups (Hobson et al. 2021b; Smith and Pinter-Wollman 2021).

A major question that advances in data collection and analysis can allow us to tackle in new ways is the relationship between social networks and cognition. Social networking strategies are likely to have cognitive constraints, and insights into cognitive abilities can come from identifying the strategies that underpin social network structure (Hobson et al. 2019; Hobson et al. 2021a). For example, dominance networks can reveal whether individuals assess third-party relationships and cooperation networks can reveal whether helping decisions integrate social experiences over time.

Cognitive constraints might also shape if and how individuals compare the quality of different partners or opponents, or alternatively, whether they use relatively simple heuristics. For example, winner and loser effects occur when fighters make decisions regarding a current opponent simply based on whether they often won or lost with past opponents (Dugatkin and Druen 2004). The analogous effect for cooperation is called generalized reciprocity which occurs when individuals are more helpful simply after experiencing being helped (Rutte and Taborsky 2007). Winner and loser effects can have long-term consequences (Laskowski et al. 2016), and similarly, early-life experiences of cooperation might alter investment strategies later in life (Wu et al. 2020).

In combination with new computational and data collection methods, research on the social lives of animals is poised for new scientific breakthroughs. Having both collaborated with researchers in math, engineering, and computer science, we strongly encourage communication with researchers from different academic fields (*e.g.* ecologists and computer scientists) and sub-fields (*e.g.* primatologists and ornithologists) who can bring together new tools, skills, and perspectives. We urge researchers interested in animal social systems to craft their own collaboration network strategies to better connect across scientific communities and better take advantage of approaches and concepts from other fields. Combined, work with both animals and humans will allow for more explicit testing of the general patterns in the evolution of sociality, especially the hypothesized link between the evolution of social and cognitive complexity.

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26

CHANGING IDEAS ABOUT MATING SYSTEMS

Nancy G. Solomon and Brian Keane

Mating systems can be viewed as epiphenomena observed at the population level resulting from the behaviour of males and females attempting to maximize their reproductive success. These male–female interactions occur in particular demographic, social and environmental contexts and interspecific or interpopulation differences in mating systems may reflect differences in one or more of these factors as well as variations in life-history traits and genetics.

There is disagreement about what constitutes a mating system. Many researchers thought of mating systems as consisting of who spends time with whom, which individuals (if any) engage in parental care and who mates with whom. In contrast, Kappeler (2019) stated that the mating system is one aspect of a species' social system and encompasses who mates with whom. This component of the mating system is viewed as distinct from other components that have been previously included as aspects of mating systems. Specifically, Kappeler says that parental care, if it occurs, should be distinct from the mating system as should social organization (group size, composition and relatedness) and social structure (interactions that occur within a social unit including pair bond formation).

Classification

Classification of mating systems has been inconsistent due to differences in the conceptual framework used to define them. Verner and Willson (1966) and Emlen and Oring (1977), in their seminal papers, classified mating systems by the number of mates per individual (Table 26.1). They focused on the outcome resulting from spatial and temporal distribution of resources required by females and the ability of males to monopolize access to females. Shuster and Wade (2003: see Tables in Chapter 9), proposed a more complex classification scheme because they thought the traditional approach seemed too static and believe there are many different ways for mating systems to evolve. They viewed mating systems as dynamic, able to change, and even evolve, rapidly. They proposed that, even when subtle changes in spatial and temporal distributions of mating opportunities occurred, mating systems could change due to differences in intersexual fitness, which are responsible for shaping male and female mating phenotypes through the opportunity for selection (see Table 6.1 in Shuster and Wade 2003). Furthermore, some investigators have used adjectives to further distinguish simultaneous from sequential mating systems e.g., sequential monogamy. This lack of consistent terminology has led to different researchers classifying the mating system of the same population differently (e.g., Steyaert et al. 2012).

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Table 26.1 Traditional classification of mating systems based on number of mates compared with classification based on temporal and spatial distribution of females proposed by Shuster and Wade (2003).*

Traditional classification	*Shuster & Wade's classification*
Monogamy one male mates with one female	Eumonogamy, persistent pairs, sequential pairs, mass mating with male parental care
Polygamy one member of one sex mates with more than one member of the other sex	
Polygyny one male mates with more than one female	Attendance polygyny, iteroparous mass mating, cursorial polygyny, iteroparous exploded leks, dominance polygyny, polygynous social pairs, feeding site polygyny
Polyandry one female mates with more than one male	Attendance polyandry, nest site polyandry
Promiscuity/Polygynandry both males and females have more than one mate	Attendance polygynandry, coercive olygynandry, mass mating, dominance polygynandry, polygynandrous social pairs, classic leks, harem polygynandry, nest site polygynandry

*Note that some of Shuster and Wade's classifications are subdivided and fit under more than one traditional category. For example, mating swarms can be subdivided into those that fit under all these traditional categories.

Mating Systems and Genetic Parentage Assessment

One obvious problem with the initial classification of mating systems is that they were formulated without knowing parentage of offspring. Using genetic techniques for assessing parentage, researchers found genetic monogamy in less than 25% of socially monogamous avian species (Brouwer and Griffith 2019). Similar results were found in other taxa such as mammals when presumptive monogamous species were examined (Clutton-Brock and Isvaran 2006; Lambert et al. 2018). These findings resulted in redefining mating systems by splitting the original terms into social mating system and genetic (sometimes referred to as sexual or reproductive) mating system. Thus, we might find a population where males and females were predominantly socially monogamous but engaged in extra-pair copulations, being genetically polygynous and genetically polyandrous.

Once paternity analyses became more common, researchers found that vertebrates and invertebrates often displayed genetic polyandry (females mating with multiple males) irrespective of the social mating system. Hypotheses proposed to explain genetic polyandry focus on direct or indirect fitness benefits to females (Parker and Birkhead 2013). Mating with multiple males may 'confuse paternity', preventing male infanticide if males are not certain which offspring are theirs (Harcourt and Greenberg 2001) or enabling females to obtain paternal care from multiple males (Stacey 1982). Mating with more than one male could also ensure that females have sufficient sperm to fertilize all their ova (Boulton and Shuker 2013). Alternatively, females may obtain nuptial gifts from males, which can increase fecundity (Lewis and South 2012). Additionally, females may obtain genetic benefits such as good genes (Griffith et al. 2002), compatible genes or greater genetic diversity in offspring (Petrie and Kempanaers 1998).

Ecological, Social, and Behavioural Influences on Mating Systems

After the acceptance of individual selection, more attention was paid to sexual selection and ecological factors that resulted in different mating systems. Verner and Willson (1966) and Orians (1969) proposed the polygyny threshold hypothesis to explain whether females decide to settle on a male's territory that contains a conspecific female versus a territory without females. When a habitat varies in the resource quality (e.g., availability of food, nest sites), Orians (1969) assumed that some males would be relegated to territories of lower quality and once the highest quality male territories were occupied by one female, additional females might have greater reproductive success if they settled as a secondary female on a high-quality territory of an already paired male than with an unpaired male on a territory of lower quality. The difference in the quality of territories occupied by the paired versus unpaired males available to a new female at the time when she would be ready to select a territory is called the polygyny threshold (Verner and Willson 1966). Polygyny is expected to evolve if the polygyny threshold is exceeded frequently within a habitat.

Emlen and Oring (1977) extended these initial ideas to include additional factors. They coined the phrase "environmental potential for polygamy" to refer to the cost/benefit ratio that would allow members of one sex to control access to multiple members of the other sex. Factors that could influence this ratio include the spatial distribution of resources, the temporal pattern of female receptivity, the operational sex ratio (OSR, ratio of sexually active males to fertilizable females) and the amount of parental care required to successfully raise offspring. If critical resources were sparsely distributed, slow to be renewed or of low quality, they might not be sufficient to support more than one female with their dependent offspring on a territory. Thus, females would not be expected to tolerate conspecific breeding females. Under these conditions, it could be beneficial for a male and female to engage in social monogamy and jointly defend access to these critical resources. In contrast, if resources were patchily distributed and relatively abundant, then females could share a resource patch. Females should tolerate each other and males could monopolize access to multiple females making polygyny likely.

The degree of synchrony in female receptivity could also influence mating systems (Emlen and Oring 1977). If all females in a population were receptive at the same time and receptivity did not last very long, a male could not mate with multiple females because by the time he mated with one female, others would no longer be receptive. Under these circumstances, fitness benefits obtained by having continual access to one female could exceed benefits that a male could obtain by attempting to mate with multiple females (Tecot et al. 2016) and monogamy would be favored. In contrast, if female receptivity was asynchronous, then males would be able to court and mate with multiple females resulting in genetic polygyny.

The cost of offspring care could also influence social and genetic mating systems. Emlen and Oring (1977) thought that polygyny would be more likely if females were able to care for offspring without assistance from males (and vice versa for polyandry). Offspring care by one sex could occur if resources were so abundant that only one parent was needed to obtain sufficient resources for offspring or if only minimal care of offspring was necessary for successful rearing. But, if offspring care is time consuming, it benefits a male to remain with a female and help care for offspring, increasing their growth and survival (Kleiman 1977). When males invest heavily in offspring care, genetic polygyny should be less common than in species or populations where males do not invest as much time or effort (Fernandez-Duque et al. 2019).

The risk of infanticide also might influence the evolution of mating systems (Opie et al. 2013). When risk of infanticide is high, offspring may benefit from the presence of their father to help protect them from infanticidal conspecifics. Under these circumstances, it may benefit a male and female to be socially monogamous. However, recent evidence shows that in mammals, infanticide does not appear to be a driver of monogamy except in primates (Lukas and Clutton-Brock 2013). Similarly, predation may influence offspring survival and can influence the social mating system. The effect of predation on the social mating system has been questioned because it seems that it should not matter whether a male and female, multiple males or multiple females protect offspring (Fernandez-Duque et al. 2019).

Recently, mathematical models have shown that different mating system outcomes can be obtained depending on the assumptions underlying models and factors included in them. Models that focused on behavioural differences, (e.g., intersexual and intrasexual interactions) without regard to changes in environmental or demographic characteristics (e.g., resource distribution, OSR) resulted in different outcomes than those expected from classic mating system theory (Alonzo 2010). One model assumed that if females sequentially encountered males in proportion to male density, females would have to decide whether to accept reduced paternal care from a mated male or delay reproduction and continue to search for an unmated male. Because delaying reproduction could be costly, polygyny could be more beneficial than monogamy under most conditions. Monogamy would be adaptive for females only in very unproductive environments where adult density is low, when there is no reproductive interference from conspecific females and mortality and fecundity are similar among females (Jungwirth and Johnstone 2019). Modifying the model to include interference with mate selection by resident breeding females, decreases in reproduction or increases in mortality would increase costs of being a secondary female. These circumstances would favor monogamy at a greater range of densities.

Models focusing only on extrinsic factors such as resource distribution may also miss important causal factors, resulting in an incomplete understanding of mating system evolution (Sinervo et al. 2020). Although changes in the environment can alter the advantages of a particular mating system, evolutionary inertia from intrinsic genetic factors might prevent changes from occurring in the existing mating system. Conversely, changes in intrinsic genetic factors could alter a mating system even when there is no change in environmental factors. Furthermore, extrinsic factors such as resource availability could interact with genetic factors resulting in interspecific differences in mating systems or intrapopulation changes in mating systems.

Some classic papers on mating systems treated females as passive participants in reproductive interactions or assumed that they responded almost exclusively to resource acquisition (King et al. 2013). Since the 1980s, researchers have paid more attention to the female perspective, in particular the adaptive significance of female behaviour (e.g., mate choice) and female morphology (Jennions and Petrie 2000; Rubenstein 2012). For example, female black-capped chickadees were more likely to seek additional matings if their mate was low ranking (Smith 1988). Observations like these led to the hypothesis that females may have morphological and/or physiological adaptations to select which male's sperm fertilized their eggs (i.e., cryptic female choice) and that this behaviour, which benefited females (Eberhard 1996), influenced the mating system.

It is likely that intersexual conflict over sociosexual behaviour that would result in the greatest reproductive success for each sex could occur. Males could benefit by polygyny, even if it reduced paternal care, if their overall reproductive success was greater. When paternal care is important for offspring growth and survival, females may suffer a cost from sharing a male and his territory. Alternatively, even if females obtained greater reproductive success by mating polyandrously, males would likely suffer a cost from sharing paternity with another male. Males would benefit more by mating monogamously than by sharing paternity. Thus, the mating system that is displayed would be responsive to costs and benefits to both sexes as well as to environmental circumstances (Davies 1989).

Intraspecific Variation in Mating Tactics

Mating systems have traditionally been portrayed as species-specific characteristics, even though researchers recognized that some males and/or females varied from the modal mating system. For example, species of birds have been classified as polygynous if at least 5% of the males in the study population had more than one mate simultaneously (Verner and Willson 1966). Thus, 95% of males could engage in monogamy or polyandry and the species would still be called polygynous!

Variation within mating systems did not gain much attention until researchers realized that there was much more inter- and intrapopulation variation than had been recognized (Lott 1991). Now we realize that animal mating systems may result from reproductive tactics of individuals expressed in the context of sexual selection (Gross 1996; Shuster et al. 2019). Thus, inter- and intrapopulation variation in mating behaviour is not surprising when individuals respond to changes in intrinsic (genetics, experience) factors, extrinsic (demographic, environmental) factors or both (Lott 1991). Today we refer to the variation in tactics used by males or females to obtain matings as alternative mating tactics (AMTs). A classic example is bluegill sunfish (*Lepomis macrochirus*) where some males are territorial and parental, and others mimic females (pseudofemales) or sneak matings (sneakers) (Gross 1982). Males displaying all three AMTs can fertilize eggs but parental males obtain on average 81% of all paternities (Fu et al. 2001).

Neurogenetic Influences on Mating Systems

Researchers have begun to discover the hormonal, neural and genetic traits underlying social and genetic mating systems. Certain aspects of mating systems such as territorial defense, social recognition and memory can be influenced by the neural pattern and density of oxytocin and vasopressin receptors (Oldfield et al. 2015; Ophir 2017), although the interpretation of results from interspecific comparisons is not always simple (Oldfield et al. 2015). Oxytocin is thought to be important in pair bond formation and also in social recognition (Numan and Young 2016). Additionally, dopamine and two of its receptors appear to be an important influence on pair bonding in both sexes (Fischer et al. 2019). Finally, some evidence suggests that estrogen receptor alpha is also involved in mating systems (Cushing and Wynne-Edwards 2006).

Young et al. (2019) reported similarities in gene expression among males of monogamous species from unrelated taxa that differed from the pattern displayed by males of non-monogamous species. The similar patterns of neural gene expression in diverse vertebrates could not be explained by ecological factors or evolutionary divergence times.

The neuroendocrine and genetic mechanisms underlying behaviours that affect mating systems are still largely unexplored and our current understanding is from only a few species. Thus, future research involving a greater variety of interspecific comparisons would enhance our understanding of how these mechanisms influence aspects of mating systems.

The Complexity of Mating Systems Exemplified by Prairie Voles

Although prairie voles are commonly portrayed as one of the few mammalian species that are monogamous, their social and genetic mating systems are not fixed species-specific attributes.

Social Mating System

Prairie voles, *Microtus ochrogaster*, are herbivorous rodents that inhabit grasslands of north central North America and have become a model organism for studying monogamy in mammals because they display characteristics proposed to define a monogamous mating system (Carter and Getz 1993; Carter et al. 1995). Males and females are not sexually dimorphic and many form pair bonds. Male–female pairs jointly defend their nest and territory from conspecifics and also engage in biparental care of offspring.

Although the modal mating system is described as social monogamy, adult prairie voles also can be found living alone or in groups consisting of more than two adults sharing a nest with or without juveniles (Getz et al. 1993). Most residents that live singly are thought to result from mortality of one member of a male–female pair, often from predation (Getz and McGuire 1993). In addition, some males and females are nonterritorial (wanderers) and do not associate with only one nest site (Getz et al. 1993; Solomon and Jacquot 2002). Groups typically form from a breeding pair plus philopatric adult offspring (extended family groups, Getz et al. 1993). All these social units have been commonly observed within the same population and the frequency of these social units varies temporally within populations as well as geographically among populations (Getz et al. 1993; Streatfeild et al. 2011).

Genetic Mating System

Even though prairie voles are described as socially monogamous, parentage data from natural populations indicate that male–female pairs do not exhibit mating exclusivity. Solomon et al. (2004) reported multiple paternity in prairie voles based on evidence of more than one sire in litters from 5/9 (55%) females from an Illinois population. Genetic parentage data from other populations revealed that a number of males and females mated with more than one individual. Multiple paternity was detected in 28% (7/28) of litters in a Kansas population and 60% (35/58) of litters in an Indiana population (Streatfeild et al. 2011). Males in an Indiana population that sired offspring (n = 38) bred with an average of 1.5 females (Keane et al. 2014). Similarly, among Illinois voles maintained in outdoor enclosures, males that sired offspring (n = 21) bred with an average of 1.8 females (Keane et al. 2017).

Ecological, Social, and Behavioural Influences on Mating Systems

Both the social and genetic mating systems of prairie voles are affected by ecological factors such as population density and the distribution and abundance of vegetation. In outdoor enclosures, prairie voles tend to live in male–female pairs at low-moderate population density. An increase in philopatry of offspring with increasing density resulted in a significant increase in the proportion of social units that were groups, although they typically still contained only one breeding pair (Lucia et al. 2008). However, the addition of supplemental food did not affect the social mating system, which remained monogamous (Cochran and Solomon 2000).

A two-year study of natural populations in Indiana and Kansas revealed geographic differences in the social and genetic mating systems (Streatfeild et al. 2011). Male home ranges in the Indiana population were about twice the size of female home ranges and overlapped multiple female home ranges, suggestive of a polygynous mating system, while in Kansas male and female home ranges were similar in size and primarily overlapped one opposite-sex conspecific as typically found in monogamous mating systems. Only 31% of individuals were socially monogamous and 40% were genetically monogamous in Indiana, while in Kansas a greater proportion of individuals were socially (46%) and genetically (72%) monogamous (Figure 26.1). Vegetation provides cover and food for prairie voles and in Indiana most vegetative variables measured (e.g., percent cover, height, preferred food)

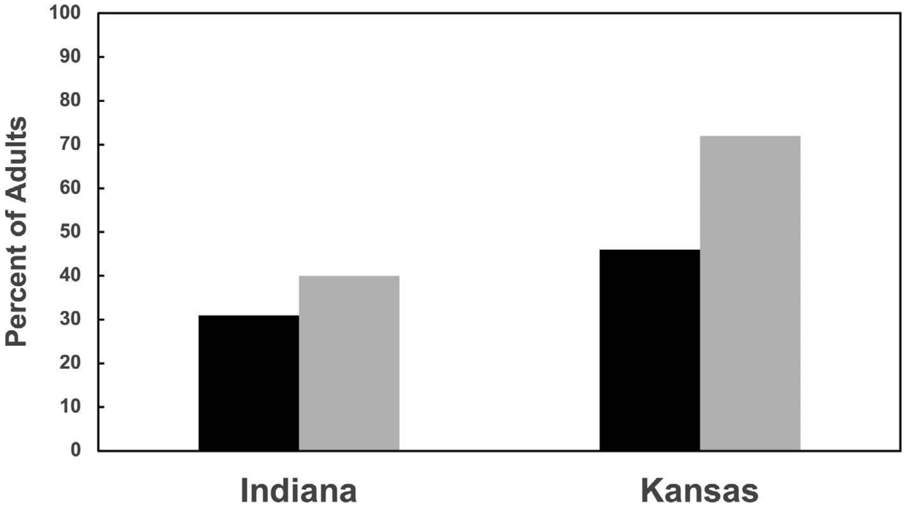


Figure 26.1 Percent of adults that were socially (black) and genetically (grey) monogamous in an Indiana and Kansas population.

showed greater degrees of spatial aggregation than in Kansas. A greater degree of spatial autocorrelation in vegetation in Indiana was associated with significant positive autocorrelations of female home ranges and nest site locations. These results are consistent with expectations from Emlen and Oring (1977) that social and genetic monogamy should be less common in locations like the Indiana site where resources required by females, and females themselves, are more aggregated. However, in this study the impact of the vegetation on the mating systems could not be distinguished from that of population density as adult densities in Kansas ranged from low to medium (27–44 voles/ha) while those in Indiana ranged from medium to high (40–80 voles/ha).

Mate guarding has been proposed as a driver of monogamy because the fitness benefits a male would obtain from having sole mating access to one female may outweigh the benefits that a male could obtain by mating with multiple females (Tecot et al. 2016). However, a study of prairie voles living in enclosures provided no support for the hypothesis that a female's male social partner reduces the likelihood of her breeding with other males because there was no difference in the percentage of litters with multiple paternity among litters produced by single females (13/39; 33%) compared to litters produced by females with a male social partner (8/30; 27%, Lichter et al. 2020). In this same study, unpaired males were more likely to sire offspring with more than one female than paired males, suggesting that paired males sacrifice opportunities to mate with more females. However, breeding with fewer females does not necessarily mean that paired males have lower reproductive success than unpaired males. For example, the paternal care provided by paired males may increase survival of their offspring relative to unpaired males that were more likely to breed with unpaired females.

Factors other than the presence of the male social partner must explain the lack of a difference in the frequency of multiple paternity in paired versus unpaired females. In another study of enclosed populations, neither familiarity nor relatedness influenced the social mating system as measured by pair formation, but familiarity influenced the frequency of multiple paternity in paired females (Lucia and Keane 2012). Females were significantly more likely to breed with unfamiliar males, but females that produced offspring with a familiar male were also significantly more likely to have litters with multiple paternity (4/5 litters) than females producing offspring only with unfamiliar males (6/27). These results are consistent with the hypothesis that females are using familiarity as a proxy for relatedness to avoid inbreeding and that the "perceived" quality of a female's social partner can influence the genetic mating system.

Alternative Mating Tactics

In prairie voles, two alternative tactics, residents and wanderers (sometimes called floaters or satellites, Taborsky et al. 2008) have been commonly reported in adult males and females in natural populations (Getz et al. 1993; Streatfeild et al. 2011), as well as in populations in outdoor enclosures (Solomon and Jacquot 2002; Ophir et al. 2008). Resident females or males typically form a pair bond with one opposite-sex adult, reside at one nest, jointly defend a territory, and display biparental care of offspring (Getz et al. 1993). Wandering prairie voles do not reside at one nest and, to our knowledge, do not form a pair bond with one opposite-sex conspecific (Getz et al. 1993; Solomon and Jacquot 2002). Shuster et al. (2019) found geographic and temporal differences in the percentage of residents and wanderers in Kansas and Indiana populations. In east central Illinois, the majority of adult male prairie voles were territorial residents (males 54–68%, Getz et al. 1993) but the opposite was found in populations in Kansas and Indiana (only 29% & 34% residents, respectively, Shuster et al. 2019). In the Illinois and Kansas populations, the majority of females were residents (76–81% and 55%, respectively) but residents were the minority in Indiana (42% residents). Residents were more common in seminatural enclosed populations (males 82–97%, females 92–99%, Solomon and Jacquot 2002). Some of the variability may be due to density or other factors that are unknown at this time. Furthermore, these AMTs are not fixed patterns of behaviour because individuals switch tactics during their lifetime.

It has been suggested that prairie voles adopting a wanderer tactic experience lower average fitness than residents and are simply "making the best of a bad job" (Ophir et al. 2008; McGuire and Getz 2010). To test this hypothesis, three years of genetic parentage data from natural populations in Indiana and Kansas were used to examine the variance in fitness of individuals displaying these two AMTs (Shuster et al. 2019). The average fitnesses of males or females expressing resident or wanderer mating tactics were equivalent, within and among years within each location, failing to support the hypothesis that wanderers were "making the best of a bad job". The persistence of these two AMTs in the Indiana and Kansas populations appear to be due to negative frequency-dependent selection acting on mating phenotypes with resident males and wanderer females producing offspring primarily in genetically monogamous relationships, while wanderer males and resident females were more likely to engage in genetic polygyny. Despite environmental differences between locations, selection operated on male and female mating tactics similarly in each site.

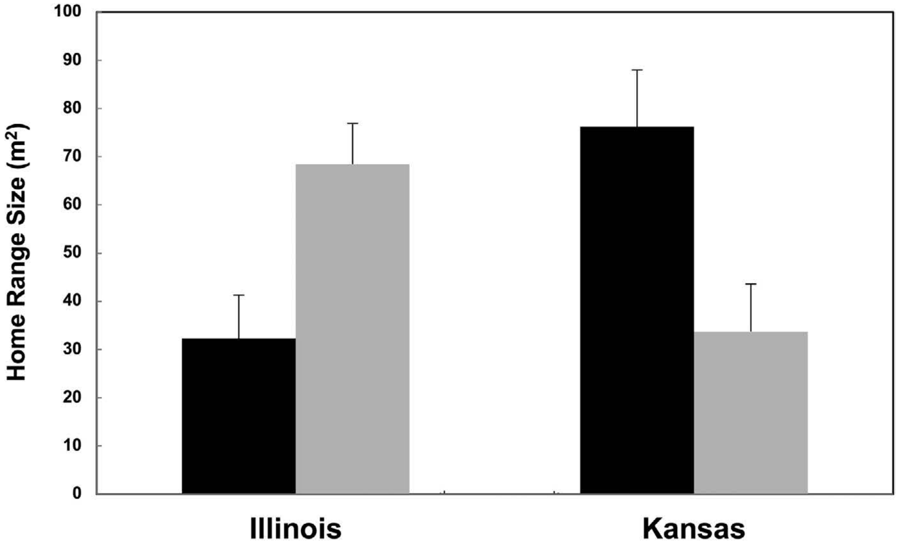
Neurogenetic Influences on Mating Systems

Laboratory studies have identified several neural mechanisms that mediate the expression of social behaviour in prairie voles, but only recently have researchers examined the relationship between neural mechanisms and social behaviour in field populations. The neuropeptide arginine vasopressin influences sociosexual behaviour in male mammals through its action on the vasopressin 1a receptor (V1aR, Goodson and Bass 2001). In prairie voles, polymorphism in the length of a microsatellite within the regulatory region of the gene (*avpr1a*) encoding for V1aR predicts differences among males in the expression of V1aRs in specific areas of the brain known to influence sociosexual behaviours. Specifically, in laboratory trials, males with longer *avpr1a* microsatellite alleles exhibited greater expression of behaviours characteristic of social monogamy (e.g., partner preference, paternal care) relative to males with shorter *avpr1a* microsatellite alleles (Hammock and Young 2005). In contrast to lab results, field studies with voles from natural populations in Indiana and Kansas have not detected any evidence that a male's *avpr1a* genotype predicts variation in indices of social monogamy (male home range size, social association with females, Mabry et al. 2011; Keane et al. 2014). Male *avpr1a* genotype was not correlated with genetic monogamy in 4-week studies of populations in Indiana and Kansas (Mabry et al. 2011), but in a subsequent 15-week study of the Indiana population, males with longer *avpr1a* alleles were more likely to sire offspring with multiple females than males with shorter *avpr1a* alleles (Keane et al. 2014).

When Illinois and Kansas voles were bred to produce male offspring that possessed either two *avpr1a* microsatellite alleles that were at least one standard deviation longer or shorter than the mean allele length and the offspring were released into enclosures, Illinois males with long *avpr1a* alleles had significantly smaller home ranges and significantly greater home range overlap with the female they overlapped with most compared to males with short *avpr1a* alleles (Figure 26.2, Keane et al. 2017). Males from Kansas showed the opposite pattern. Illinois males with long *avpr1a* alleles sired offspring with an average of about two females compared to one female for males with short *avpr1a* alleles ($p = 0.03$, Keane et al. 2017). However, Kansas males with long or short *avpr1a* alleles sired offspring with an average of 1 female.

These results from this manipulative field experiment support the hypothesis that genetic variation at the *avpr1a* locus plays a role in mediating male sociosexual behaviour in nature. However, the relationship between specific behaviours characteristic of the social or genetic mating system and male *avpr1a* genotype is complex, likely involving other neurogenetic and environmental factors and their interactions.

Expression levels of estrogen receptor alpha (ERα) in the medial amygdala (MeA) are directly linked to socially monogamous behaviour in male prairie voles in laboratory studies. Greater levels of ERα expression in the MeA interfere with partner preferences in males and paternal care (Cushing et al. 2008). This relationship varies geographically with prairie voles from Kansas displaying



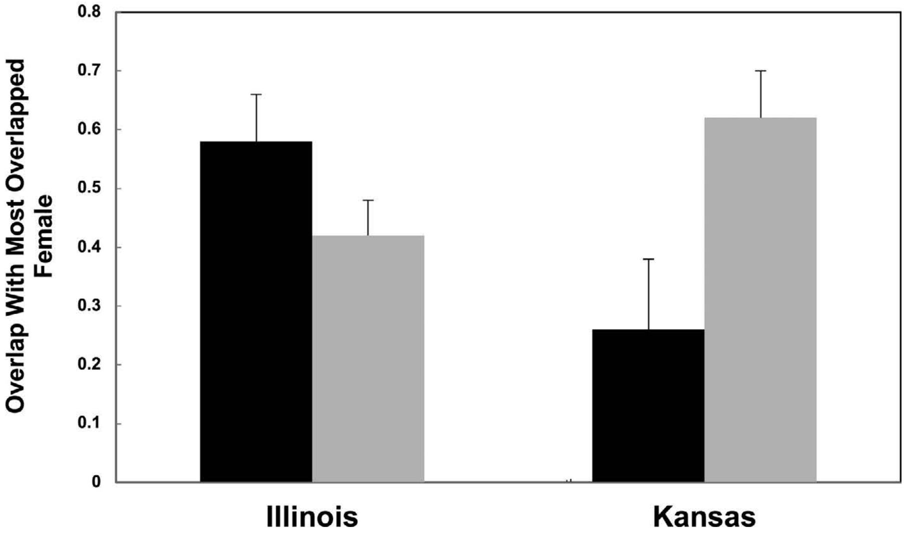


Figure 26.2 (a) Mean home range size ($m^2 \pm 1$ SE, $F_{1,\ 28.8} = 16.63$, $p = 0.0003$) and (b) proportion of home range overlap (± 1 SE, $F_{1,\ 18.3} = 6.68$, $p = 0.03$) with the adult female they overlapped the most for males with long (black) and short (grey) *avpr1a* microsatellite alleles from Illinois and Kansas.

significantly lower levels of pair-bonding and paternal care and expressing significantly higher levels of ERα in the MeA than Illinois males (Cushing et al. 2004). Male F_1 offspring from Kansas dams and Illinois sires (KI males) exhibit the least socially monogamous behaviour and significantly overexpress ERα in the MeA relative to males from either population (Kramer et al. 2006). When

KI males with experimentally decreased ERα expression in the MeA were maintained in outdoor enclosures with KI males with unmanipulated ERα expression (control males), KI males with decreased ERα had stronger associations with one female, smaller home ranges that overlapped fewer females, and greater home range overlap with one female than the control males (Lambert 2018). The KI males with experimentally decreased ERα expression in the MeA and control KI males did not differ in their likelihood of being genetically monogamous. These findings demonstrate that experimentally decreasing ERα expression in the MeA caused increased socially monogamous behaviour in a field setting, supporting the idea that changes in the social brain network (SBN, sensu Prounis and Ophir 2020) can influence the social mating system.

Conclusions

There is still not agreement about what behaviours should be considered as aspects of mating systems. Additionally, we still do not understand which factors are important in the evolution and maintenance of social and genetic monogamy (Klug 2018), which is true for mating systems in general. In the future, studies in which multiple factors are examined simultaneously as well as comparative mechanistic studies are critical in identifying mechanisms shared among taxa and the variation necessary for adaptations resulting in the behavioural diversity we observe in animals.

Prairie voles are generally portrayed as one of the few monogamous mammals, but their social and genetic mating systems display considerable geographical and temporal variation resulting from individual responses to a complex interaction of extrinsic (e.g., population density, food resources) and intrinsic (e.g., neurobiological) factors to maximize their reproductive success. While laboratory and field studies have examined many factors that influence prairie vole mating systems, the challenge for future research is to conduct integrative studies of combinations of these factors in field populations.

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27

HUMAN MATE CHOICE

Jan Havlíček, Zuzana Štěrbová, and Zsófia Csajbók

Introduction

Human mate choice in many ways follows the general evolutionary principles which apply to other species. The key theoretical assumption is based on the parental investment theory, which predicts that the sex that invests more into reproduction will be more selective. In humans, as in other mammals, it is the females who shoulder the reproductive investment in the form of pregnancy and breastfeeding. As expected, women are thus on average choosier. For instance, in a classical experiment by Clark and Hatfield (1989), confederates invited unacquainted opposite-sex individuals for either a cup of coffee or sex. Not surprisingly, there were no sex differences in responses to an invitation for a non-alcoholic beverage but in willingness to have uncommitted sex, the difference was striking: 69% of men agreed, while virtually no women did. On the other hand, although the minimum male investment in reproduction is the sexual act itself, relatively high levels of paternal investment have been observed in virtually all human populations. Still, the form (e.g. resources, knowledge, and defence) and extent of paternal investment varies highly both between and within populations (Geary 2000). Women thus also seem to be highly selective.

There is a lively ongoing debate about the phylogeny of human mating systems. In other apes, we find monogamy/polyandry in gibbons, polygyny in orangutans and gorillas, and promiscuity in chimpanzees (Dixson 2015). In humans, mating systems vary across cultures, with polygyny/monogamy being the most widespread, followed by monogamy only, with polyandry/monogamy being rare (see also Chapter 26 in this volume). It should be noted, though, that in virtually all cultures that permit polygyny, most adults still form monogamous pairs. Moreover, the cultural rules of mating need not fully overlap with the reproductive, sexual, and social forms of mating.

The specifics of human mating are linked to culture as a key aspect of human ecology. There is a general preference for in-group individuals both as social and romantic partners. Many aspects of human mate preferences thus include in-group markers, which may considerably vary across cultures and fluctuate over time (Little et al. 2011). This is illustrated by the general tendency to manipulate own appearance in various ways, from hairstyles and body decorations all the way to various permanent alterations, such as cranial or foot deformations (Davis and Arnocky 2022).

A special and possibly unique aspect of human mating has to do with the involvement of other individuals apart from the choosers themselves. In most cultures, offspring are not free to choose their mate. Involvement of other individuals, such as parents or wider kin, may take various forms ranging from arranged marriage with no input of the couple concerned to restricted choice or group

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decision. To the best of our knowledge, there is no evidence of any analogical 'group sexual selection' in other species (Apostolou 2017).

In this chapter, we summarise the main findings on human mate choice using the evolutionary framework. Where possible, we suggest the most likely evolutionary mechanisms underlying the evolution of relevant psychological characteristics. To highlight which aspects of human mate choice are shared with other species or are unique to us, we turn to a comparative and phylogenetical perspective. We start by introducing the concept of mate preferences and characteristics which humans tend to prefer in potential mates. Then we turn our attention to the main sources of variation in mate preferences, such as sex, mate value, and culture. We outline the individual development of mate preferences, including some specific learning processes such as the imprinting-like effect. We introduce the most influential models of mate choice and review evidence on assortative mating, including possible mechanisms of mate assortment. Finally, we discuss parental involvement in human mate choice. The chapter is closed by a brief summary with some pointers to major gaps in current knowledge and possible future research avenues.

We focus on the initial phases of mating, such as mate preferences and mate choice, leaving aside other vital topics, such as courtship, love, attachment, mate retention, parenting, and relationship dissolution. They are all crucial for successful rearing of the offspring, but are covered elsewhere (e.g. Fletcher et al. 2019).

Mate preferences

Mate preferences can be viewed as a set of cognitive abilities including mental representations of an ideal/preferred partner, which evolved to guide evaluation of prospective or alternative mates. It is assumed that preferred traits provide cues to potential partners' valuable qualities, such as those related to genetic make-up, fertility status, health, or ability to provide resources and parental care. In non-human species, mate preferences are usually studied using the experimental preference paradigm, an approach widely used in research of physical attractiveness. In humans, another widely used approach is based on rating scales for various characteristics, whose results are entered into some dimension-reducing method, such as factor analysis (Csajbók and Berkics 2017). This paradigm capitalises on the fact that mate preferences can be verbally communicated, but also – somewhat controversially – assumes that people are fully conscious of their preferences (Miller and Todd 1998). Models of mate preferences usually include (i) sociodemographic, (ii) psychological, and (iii) physical appearance characteristics.

Each individual mate preference includes an absolute and a relative component. The absolute component shows agreement across individuals with some optimal value, while the relative component takes into account the value of chooser's trait and is expressed as preference for similarity or dissimilarity. For example, women tend to prefer tall partners, but actual preference is modulated by women's own height (Pawlowski 2003). In the following section, we focus on absolute preferences; relative preferences are reviewed in Section 5.1.

Sociodemographic characteristics

There is a systematic preference for high status individuals. The two major sources of status are prestige, based mainly on social reputation, and access to or ownership of resources. The latter characteristic tends to evince the largest sex difference: it is an important component especially in female mate preferences. Interestingly, several recent studies reported that socioeconomic status may not be very significant, but those studies are based on reports from rich and industrialised countries where women often enjoy high levels of independence and are less dependent on their partner's resources. In a recent study comparing 45 countries, this finding was thus not confirmed (Walter et al. 2020).

There is also a systematic preference for age similarity, although men with increasing age prefer a higher age difference (Walter et al. 2020). In other words, men irrespective of their age tend to prefer young adult women. This is in striking contrast to other apes, where relatively mature females are generally found the most attractive (O'Connell et al. 2020).

Psychological characteristics

Psychological characteristics considered in mate choice range from the broad Big Five domains, such as agreeableness and extraversion, to relatively specific characteristics, such as jealousy and liking children. The highest importance is attributed to agreeableness, which includes characteristics such as kindness and willingness to share. Another key characteristic is emotional stability, which relates to predictability of behaviour. Intelligence is also often reported as important in mate choice because it is linked to acquisition of resources (Prokosch et al. 2009). Nevertheless, it has also been reported that there are limits to intelligence preference and extremely high intelligence is generally not desirable. A potential cue to intelligence might be the sense of humour, which is also highly valued in potential mates and in men in particular (Lippa 2007).

Physical appearance characteristics

Physical attractiveness plays a crucial role in mate preferences, with visually perceived characteristics – such as facial and body attractiveness – being perhaps most important. Highly attractive faces are characterised by high levels of prototypicality (averageness), symmetry, and in women also sexual dimorphism, i.e., femininity (Little et al. 2011). Women do not show clear preference for highly masculine faces, which suggests limits of intersexual selection for sexual dimorphism in human males (Kleisner et al. 2021). Further, we find a systematic preference for carotene-related colours and smooth skin, which perhaps serves as an indicator of health (Stephen et al. 2010). On average, men view female body attractiveness as particularly important. Attractive female bodies are characterised by a relatively low waist-to-hip ratio. In contrast to faces, there is a cross-cultural variation in adiposity preferences (Swami et al. 2010). Similarly, there is a variation in preferences for breast size, although men consistently show preference for firm breasts, perhaps as a marker of high residual fertility typical of young adult women (Havlíček et al. 2017). Attractive male bodies are characterised by relatively – but not extremely – high muscularity, particularly in the upper body (Dixson et al. 2010).

Concerning vocal characteristics, high-pitched female voices and low-pitched male voices are perceived as attractive (Pisanski and Feinberg 2017), while body odour seems to provide cues to current health status. For instance, the body odour of individuals injected by lipopolysaccharide, a common bacterial antigen, was perceived as less attractive (Olsson et al. 2014). It has also been suggested that attractiveness correlates across different sensory modalities and each may work as an ornament or backup signal (Sainani 2015). However, recent studies indicate that correlations between facial, vocal, and odour attractiveness are weak at best, which suggests a relative independence of the three modalities (Třebický et al. 2022).

Individual variation in mate preferences

There is considerable agreement in some preferred characteristics. For instance, high levels of intra- and inter-populational agreement in ratings of facial attractiveness were repeatedly reported (Langlois et al. 2000). Individual variation might derive from idiosyncratic developmental trajectories, differences in mate value, sex differences, and cultural level variation. Further, there is extensive research testing variation in mate preferences due to short-term and long-term mating contexts (e.g. Buss and Schmitt, 1993), but other scholars expressed scepticism regarding the validity of this concept in small ancestral communities where chances for short-term mating might have been limited (Havlíček et al. 2015). Numerous studies tested intra-individual fluctuations in preferences across the menstrual cycle for various fitness-related attributes such as facial masculinity, but several recent large-scale studies show that the cyclic effects are not robust or of a large magnitude (Havlíček and Roberts 2022).

Variation driven by mate value

One can conceptualise the population of individuals ready for mating (e.g. sexually mature) as a mating market. In reality, though, there is no single mating market, but numerous local ones comprised of individuals who have, due to geographical and social constraints, a realistic chance to meet (see Section 6.3.). One's mate value is then the level of one's desirability as a potential partner (Fisher et al. 2008). In contrast to others'-perceived mate value, self-perceived mate value depends on evaluation of one's own desirability. The two kinds of mate value can differ, since some individuals underestimate their own mate value, while others overestimate it. Discrepancy in perceived mate value in a couple predicts mate retention behaviour and the level of jealousy (Sela et al. 2017). Because one's mate value depends on mate preferences of others, it can be expected that self-perceived mate value is predicted by mating-relevant characteristics, such as social status and physical attractiveness. However, a recent study based on large sample confirmed this expectation only for physical attractiveness (Csajbók and Berkics 2017).

Sex differences in mate preferences

Because men's minimal obligatory parental investment to reproduction is lower than that of women, men are less concerned with their partner's willingness to invest in their offspring and more sensitive to potential partner's reproductive capacity. Men thus display more pronounced preferences for physical attractiveness, cues of fertility, and relative youth than women do (Walter et al. 2020). Women, on the other hand, are more sensitive to observable cues of potential partner's ability and willingness to provide resources, which results in higher preferences for men's status and access to resources (Li and Kenrick 2006). Further, men cross-culturally score higher on sociosexuality (the desire and willingness to engage in casual sexual relationships) and on preference for sexual variety (Schmitt 2003), while women show higher levels of regret and psychological uneasiness following casual sexual encounters than men do (Campbell 2008). These differences in sexual psychology have been interpreted as a consequence of sex differences in sexual strategies. Men, like other mammal males, can increase their reproductive outcome by having sex with numerous partners, but this does not apply to women (Buss and Schmitt 1993).

Cultural variation

The population-level variation in mate preferences might be affected by both ecological variables, such as parasitic load and environmental predictability, and cultural variables, such as economic and gender inequality, sex ratio, or collectivism versus individualism. A recent large cross-cultural study confirmed the robustness of sex differences in mate preferences for physical attractiveness and access to resources. It did not, however, confirm the effect of pathogen risk and gender equality on either sex differences or mate preferences except for a finding that with increasing gender equality, both sexes mate with partners closer in age (Walter et al. 2020).

There are numerous studies showing cultural level variation in individual mate preferences related to the level of collectivism. For instance, in more collectivistic societies such as in Eastern Asia, people tend to insist on the chastity of their potential partners, while individualistic societies such as Europe or Northern America find this characteristic largely irrelevant. A similar pattern applies to preferences for religiosity (Thomas et al. 2020).

Differences of degree have also been demonstrated, e.g. higher importance assigned to physical attractiveness and lower importance of social status in US versus Singaporean women (Li et al. 2011) and US versus Chinese participants (Kline and Zhang 2009). People also tend to vary in more specific appearance-related characteristics. For instance, in nonindustrial societies, men prefer women with higher body-mass index and higher level of waist-to-hips ratio compared to US and European participants (Swami et al. 2010).

Development of mate preferences

Individual mate preferences develop by several mechanisms, presumably during childhood and puberty. Individual experiences, and close relatives in particular, play a key role in preference formation. Parents can affect mate preferences of their offspring either directly (via e.g. inheritance of preferences and social learning) or indirectly (imprinting-like effect). Nevertheless, studies examining how partner preferences are formed and how they change during life are scarce. Individual preferences can fluctuate depending on factors such as own age or relationship and parenthood status, but in general they remain relatively stable (Bredow and Hames 2019). People also tend to choose partners consistently, that is, they have their 'type' (Štěrbová, Tureček and Kleisner 2019). Importantly, the ontogeny of mate preferences has been studied mostly cross-sectionally, so the observed variation might be due to differences between cohorts rather than age groups (e.g. due to hormonal levels).

Inheritance of preferences

One of the mechanisms by which partner preferences are formed is inheritance. Studies of this phenomenon usually employ family, adoption, or the classical twin design, which is based on the fact that monozygotic (identical) twins share virtually all their genes, while dizygotic (fraternal) twins share only about half of them (Zietsch et al. 2015). On a populational level, variance in a psychological characteristic is based on genetic components, shared environment (same for both twins, affecting them in the same way) and non-shared environment (unique for each twin, affecting each in a different way). Genes, environment, and individual characteristics are mutually correlated and affect each other. Although there are currently no genome-wide association studies focused specifically on mate preferences, research on other psychological characteristics indicates that mate preferences are based on polygenic inheritance and that such genes show pleiotropic effects. This assumption is in line with genome-wide association studies on homosexual preferences, which found two chromosomal regions associated with male homosexuality, suggesting a small contribution of particular genes to male sexual orientation (Sanders et al. 2015). Regarding mate preferences, different studies report vastly varying estimates of the genetic component, from almost zero to approx. 30%, and the same holds for the effect of familial environment (from zero to approx. 60%) (Verweij et al. 2014). Different preferences can be heritable to a different extent. For instance, a study based on 4045 British twins (Zietsch et al. 2012) showed that preferences for physical attractiveness are the most heritable (29%), followed by preferences for personality traits (25%) and health (20%), while heritability of preference for housekeeping ability is the lowest (5%). Importantly, higher heritability was found for partner preferences (approx. 20% for both sexes across various traits) than for actual choice (approx. 5% for both sexes over numerous traits), which can be constrained by numerous factors including own mate value or availability of an ideal partner.

Learning processes

Mate preferences are shaped by various learning processes, including social learning from parents via observation or imitation. For instance, social learning may play a key role in intergenerational transmission of violence against intimate partner (Hines and Saudino 2002). Another form of social learning, well documented across vertebrates, is mate choice copying, which may reduce the costs of mate search and assessment. In humans, a recent meta-analysis had shown that women tend to rate potential male partners as more attractive when they are presented alongside another woman, but no analogical effect was observed in men (Gouda-Vossos et al. 2018). Still, the effect of social learning on concrete mate preferences is rarely studied. In contrast, there is a large body of research on imprinting, defined as genetically canalised learning of parental characteristics in early ontogeny that is later used as a template in own mate choice. Sexual imprinting, first postulated by Konrad Lorenz, is based on three assumptions: sensitive period, irreversibility of imprinted characteristics, and a delay between imprinting (learning of characteristics) and behaviour (preference for those characteristics). In humans, empirical evidence for these assumptions is inconclusive, which is why researchers instead speak of an 'imprinting-like' effect (Little et al. 2003). Parent–partner similarity has been found in various characteristics, ranging from demographic (age) to physical (face, eye, and hair colour) to psychological ones (extraversion). People also prefer characteristics similar to other relatives, such as siblings (Saxton et al. 2017). Effect sizes of such similarities tend to be weak to moderate, but due to genetic relatedness (and consequent mutual similarity among relatives) it is difficult to tell whether individuals choose partners based on parent-, sibling-, or self-similarity. Importantly, a study with adopted daughters (which excluded direct genetic effects) found that they chose stepfather-similar partners (Bereczkei et al. 2004). Parent–partner similarity is promoted by a warmer relationship with the parent during childhood (see also Chapter 15 in this volume), which suggests some involvement of associative learning. Since the assumptions of imprinting are not always met in humans, preference for parent-similar characteristics could be an effect of broader preferences for familiarity. Human mate choice is further affected by negative sexual imprinting, i.e. the fact that individuals develop sexual aversion towards specific individuals (usually parents and siblings) with whom they grow up (Westermarck 1921). This effect is supported by data from kibbutzim where children who were communally reared showed little attraction to each other in adulthood (Shepher 1971). These two processes may ultimately lead to a balance between inbreeding and outbreeding.

Age-related changes

Mate preferences can vary throughout life depending on benefits to the individual and/or indirect benefits to the offspring. Besides individual changes stemming from experiences, there is also a systematic variation caused by hormonal variation, especially in infancy, puberty, and menopause. Already in the first hours of life, infants show preference for faces which adults find attractive (Slater et al. 2000), suggesting that facial preferences require little former experience. Although infants can distinguish some characteristics, such as symmetry, preferences for particular characteristics form in later childhood, especially in puberty (11–12ys) (Saxton et al. 2006). Cross-sectional research shows that preference for healthy faces increases during mid-childhood (4–9ys), levels off around puberty (10–14ys), and reaches adult levels by the age of 17 years (Boothroyd et al. 2014). Mate preferences can also be altered by the menopause: for instance, it has been found that post-menopausal women prefer less masculine and less healthy individuals than fertile women do (Little et al. 2010). In men, research found a linear decline in preference for facial femininity between 30 and 70 years of age (Marcinkowska et al. 2017), suggesting a similar effect of aging on partner preferences in both sexes. A negative association between age and mate selectivity was reported in both sexes, although the effect was stronger in men (Sprecher et al. 2019).

Mate choice models

Additive models

Mate preferences are multidimensional (including e.g. physical attractiveness, resources, warmth) but mate choice decision is a single outcome. Mate choice models investigate which algorithms capture these cognitive integrations most accurately. Some animal studies suggest an additive model of mate preferences, where desirability of a potential partner is predicted by the overall sum of relevant characteristics

(Figure 27.1), which should thus indicate the most desirable potential partner. For instance, female preferences for sword length and body size in green swordtail (*Xiphophorus helleri*) appear to follow an additive integration (Rosenthal and Evans 1998). For humans, such a simple additive model is perhaps too simplistic because the importance of particular mate preferences can vary considerably and therefore also influence overall desirability to a different extent. This is captured by the weighted additive model, where each mate preference is characterised by a certain coefficient and particular preferences therefore contribute to overall desirability unequally. There is also evidence for a nonlinear relationship between the level of a characteristic and its effect on partner desirability, whereby desirability is the highest around an optimal level of the characteristic (Gignac and Starbuck 2019).

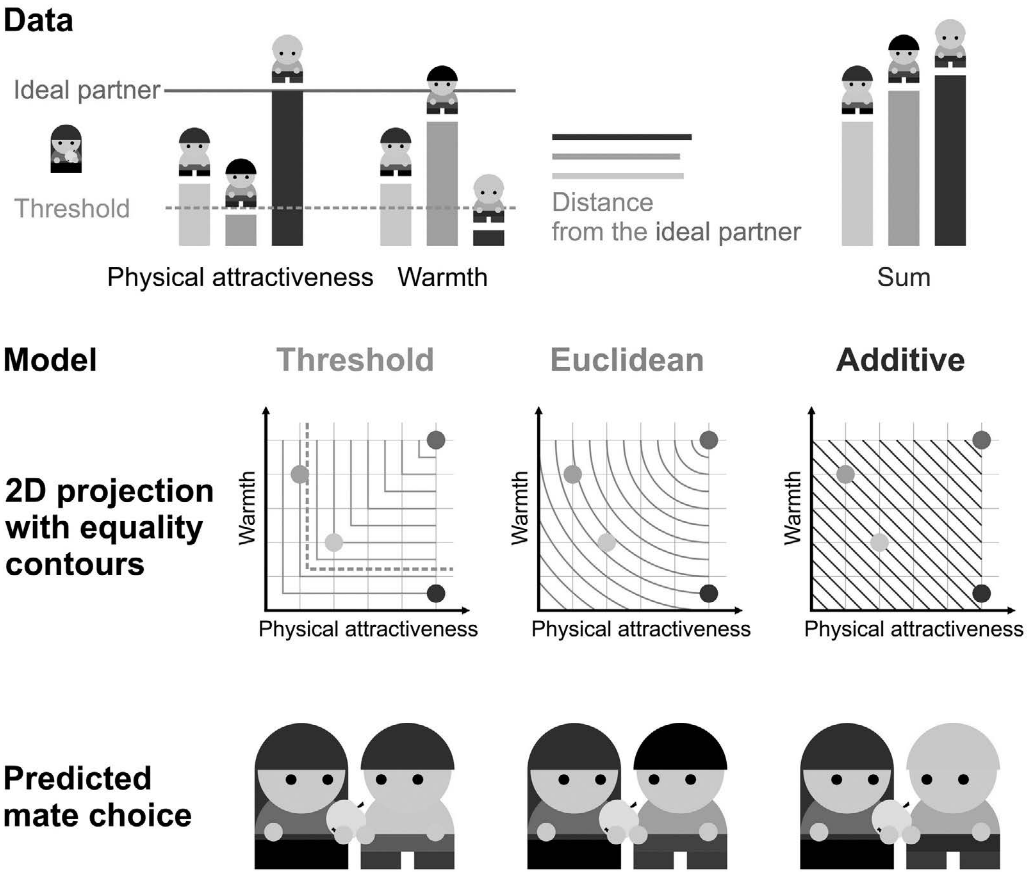

Figure 27.1 An illustrative depiction of the Threshold, Euclidean, and Additive mate preference integration models. The upper panel shows three potential partners varying in Physical attractiveness and Warmth. The Threshold is marked by a dashed line and the Ideal partner preferences of the chooser by a line. The most desirable partner, according to Euclidean distance, is marked by the shortest line and the Sum of the characteristics by the highest bar. The middle panel shows the Cartesian projection of the two characteristics with equality contours predicting desirability according to the three integration models. Dots show characteristics of the three potential partners and the Ideal partner according to the chooser. The most desirable partner according to the individual integration models is the lowest number of contour lines from the Ideal partner. The bottom panel depicts predicted mate choice according to the individual models marked by Paris's apple. The Threshold model predicts that the only individual who passes a certain threshold in both characteristics is considered acceptable, the Euclidean model predicts that the most desirable is an individual closest to Ideal partner, and the Additive model predicts that individual with the highest overall sum is the most desirable.

Threshold models

Another influential model predicts that mate preference integration is based on thresholds (Figure 27.1). This model assumes that only individuals who exceed a certain threshold for each preferred characteristic are acceptable potential mates. The individual thresholds might be adjusted according to one's mate value and partner availability. A simple threshold model assumes that a potential partner is screened for all characteristics simultaneously. A sequential threshold model, on the other hand, simulates a courtship period during which individuals screen the potential partner's characteristics one after another because some characteristics can be assessed only after achieving some level of familiarity (Miller and Todd 1998). This sequential threshold model was, however, criticised because it is much more time-consuming than parallel processing models (Conroy-Beam and Buss 2017, see also Chapter 14 in this volume). Other research suggests that people have certain partner ideals to which they compare their potential and actual partners (Fletcher et al. 1999).

Euclidean models

Recent research suggests that human mate preference integration may follow a Euclidean algorithm (Conroy-Beam et al. 2019). It takes into account the multidimensionality of mate preferences and relevant partner characteristics (Figure 27.1). Euclidean models position potential partners in a multidimensional space according to their characteristics. These are then compared to ideal partner characteristics in the same multidimensional space. Higher desirability of potential partners is equivalent to shorter Euclidean distance from the ideal partner in this multidimensional space. Such models perform particularly well when compared with other mate choice integration models – such as the threshold and additive models – in studies that use simulated agents. Overall, Euclidean integration offers a better description of mate desirability than other models do (Conroy-Beam et al. 2019).

Positive assortative mating

One of the most prominent coupling patterns across all taxa is assortative mating, that is mating based on self-similarity (positive assortative mating, homogamy) or dissimilarity (negative assortative mating, heterogamy, complementarity). A meta-analysis based on data from 254 species in five phyla showed that the mean strength of assortment is r = 0.28. Positive assortative mating has been observed far more often than negative assortative mating (Jiang et al. 2013) and in humans, homogamy is overwhelmingly more prevalent than heterogamy (Štěrbová and Valentová 2012). The most frequently reported example of heterogamy is preference for partners dissimilar in the major histocompatibility complex (MHC), which results in MHC-heterozygous offspring. In humans, however, a recent meta-analysis provided little support for these preferences (Havlíček et al. 2020) and actual human couples show random assortment in MHC (Croy et al. 2020).

The strongest similarity between partners was found in sociodemographic (age, educational level, religion), followed by psychological (attitudes, values, personality) and physical (face, body height, obesity) characteristics (Luo 2017). Homogamy usually has a weak but positive impact on relationship satisfaction, stability, and reproduction (Tregenza and Wedell 2000). It has been found that with respect to some characteristics (e.g. personality), own characteristics have a stronger impact on relationship satisfaction than dyadic similarity does, while in other characteristics (e.g. social skills), homogamy played a more important role (Dyrenforth et al. 2010). The effects of homogamy on relationship satisfaction should thus always be controlled for own characteristics. Homogamy can also have a negative impact on relationship outcomes, for example in the case of alcoholism or antisocial behaviour (Rhule-Louie and McMahon 2007). Homogamy can arise due to active (preferences for similarity) or passive (proximity effect, a by-product of competition and convergence) mechanisms.

Preferences for similarity

Couples' homogamy may be the consequence of self-similarity preferences (active assortment) (Figure 27.2), which includes preference for the same ethnicity, religion, education, or various attitudes, such as political orientation (Luo 2017). Moreover, people tend to prefer individuals with psychological characteristics similar to their own. Two distinct causal relations between self-similarity and

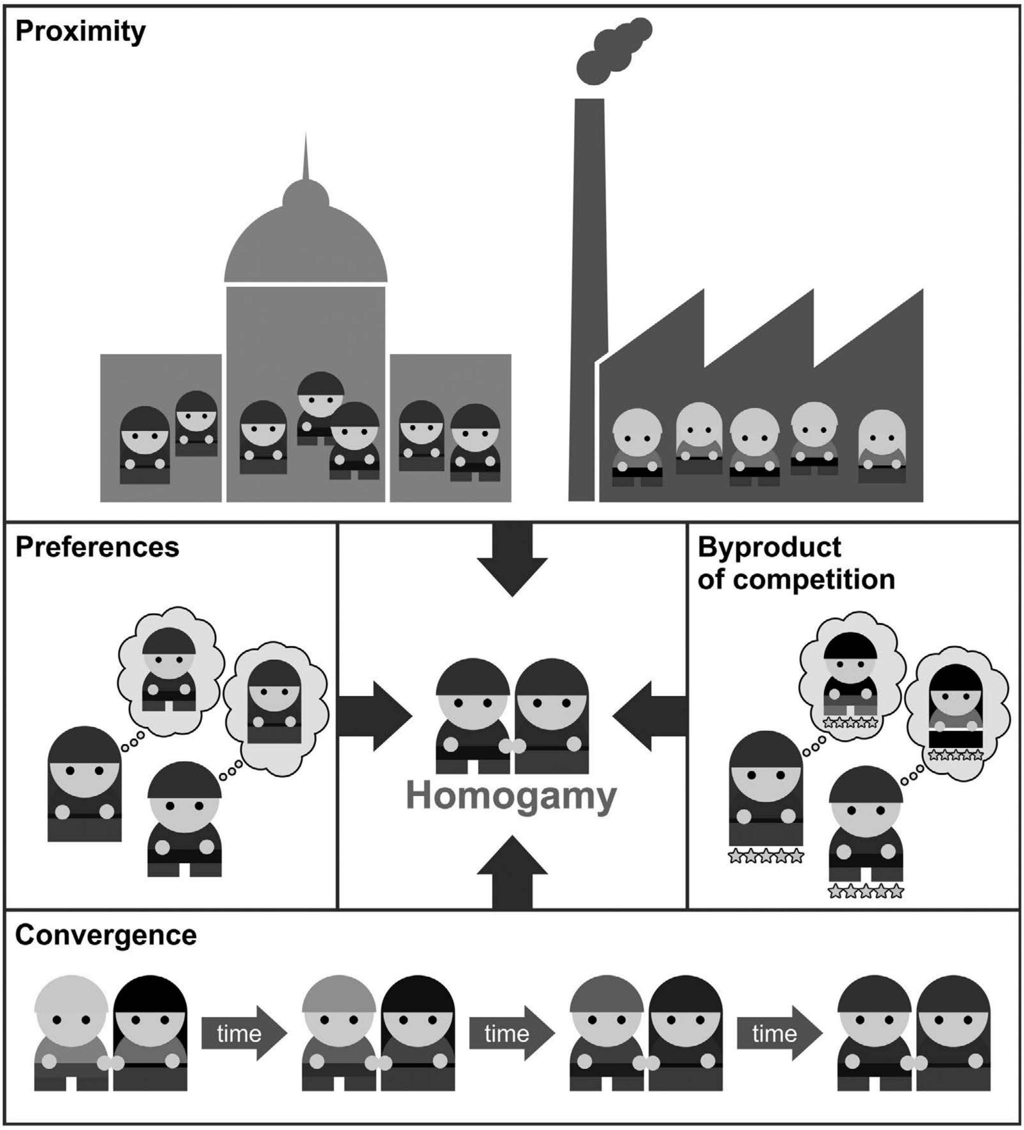

Figure 27.2 Schematic depiction of four major mechanisms of positive assortative mating (homogamy). Homogamy can emerge due to geographical and social proximity (i.e., tendency to meet similar individuals more likely) (top). People may prefer individuals similar in various characteristics (left). Homogamy can also be a by-product of positive assortment in mate value (right). Finally, partners can become more similar over time due to shared environment (convergence) (bottom). Note that the individual mechanisms are not mutually exclusive and may contribute to couples' similarity in various characteristics to a varying extent.

attraction have been proposed: according to the similarity-attraction hypothesis, more self-similar individuals are perceived as more attractive, while according to the attraction-similarity hypothesis, attractiveness increases perceived similarity (Morry 2005). Additionally, it has been found that preference for homogamy is higher than actual homogamy and discrepancy between preferred and actual homogamy is greater in homosexual individuals, perhaps due to a restricted mating market (Štěrbová et al. 2017). On the other hand, homogamy in BMI within couples was present even after controlling for preferences for obesity and BMI (Fisher et al. 2014). These results suggest that other assortative mating mechanisms are also present (see Section 5.3.). Finally, preference for self-similarity is not restricted to mate choice (homophily was found for instance in pet choice; Payne and Jaffe 2005) and since the objects of self-similarity preference are not specific, this phenomenon may be due to a more general mechanism of familiarity (i.e. liking of known objects).

By-product of competition

Homogamy can arise as a by-product of competition for the most attractive potential partners (see Section 3.1.) (Figure 27.2). This mechanism assumes an interindividual agreement on partner preferences (consensus on who is rated as more or less attractive). People make compromises between their ideal and potential partner until a potential partner is willing to establish a relationship with them based on their mate value (Hunt et al. 2015). Mutual choice of individuals with a similar mate value thus leads to their similarity irrespective of preferences. A study on Euclidean mate value showed that people with a high mate value have higher ideal standards, their partners have higher mate value, and discrepancy between their preferences and actual choices is smaller (Conroy-Beam et al. 2019).

Proximity effect

Couples' similarity can result from geographical and/or social proximity (social homogamy) (Figure 27.2). Social homogamy assumes a socially stratified society, where people are more likely to meet each other at certain places (school, work, neighbourhood) and individuals attending such places (e.g. school) are frequently similar in some characteristics. If they find a partner there, their homogamy is a by-product of the meeting place and not necessarily the result of active assortment. It has been reported that the proximity effect plays an essential role in IQ and educational assortment (Nielsen and Svarer 2009). Online studies, which are relatively free of geographic and social constraints, can distinguish between the proximity and preference effects. Couples who met online indicate self-similar preferences irrespective of geographical and social constraints (Gonzaga et al. 2010). Research found homogamy in couples even after controlling for sociodemographic characteristics, which suggests that the proximity effect is not the only mechanism affecting self-similarity (Watson et al. 2004). It is, however, important to note a possible link between proximity and preferences, which can arise simply due to mere exposure effect (i.e. affinity to familiar objects). It seems therefore that these two mechanisms cannot be fully disentangled.

Convergence

Partners can also become increasingly similar over time due to cohabitation, similar routines, diet, etc. (Figure 27.2). Higher facial similarity of couples was found on their 25th anniversary than during their honeymoon, which suggests a convergence of physical appearance (Zajonc et al. 1987). In contrast, longitudinal studies on personality, values, and attitudes revealed almost no effect of relationship length on homogamy (Caspi and Herbener 1993). It should be noted that convergence may be primarily a mechanism of relationship maintenance instead of relationship formation. In other words, less homogamous couples may break up more frequently (Schwartz and Schwartz 2010), which is why observed similarity in couples with longer relationship length need not be the result of convergence.

Parental involvement

Humans engage in group mate choice characterised by involvement of other family members. Humans are specific in including affinal relatives (i.e. relatives by marriage) in their families, so that marriages join not only two individuals but their entire families (David-Barrett 2019). A new partner becomes a new family member and the entire family must get along with him or her, which is why involvement of more experienced relatives, such as parents, can benefit both the couple and the family. From an evolutionary perspective, relatives share common genes. Mate choice of one family member can thus affect the inclusive fitness of other relatives, which may ultimately be why people interfere in the mate choice of their kin.

Variation in parental involvement

In Western societies, mate choice is usually seen as a personal decision, but cross-cultural research suggests that this is rather an exception and worldwide, relatives often interfere in mate choice. Data from 190 hunter-gatherer societies shows that only 4% of societies report marriages based on courtship, while arranged marriage is common in a vast majority of societies (Apostolou 2017). The main forms include relatively free choice, a choice from partners preselected by parents, selection together with parents, a veto on partner selected by parents, and arranged marriage without consent (Figure 27.3). Individuals from collectivistic cultures tend to feel greater parental influence, while in individualistic societies, parental influence may take the form of interventions (Buunk 2015).

Differences in parental and offspring preferences

Partner preferences of parents and their offspring may differ (Apostolou 2013). Research shows that persons who are looking for a mate tend to focus on characteristics such as physical attractiveness and sense of humour, while their parents emphasise qualities relevant to material security and willingness to invest in a family. Parents and offspring do, however, tend to agree on evolutionary relevant

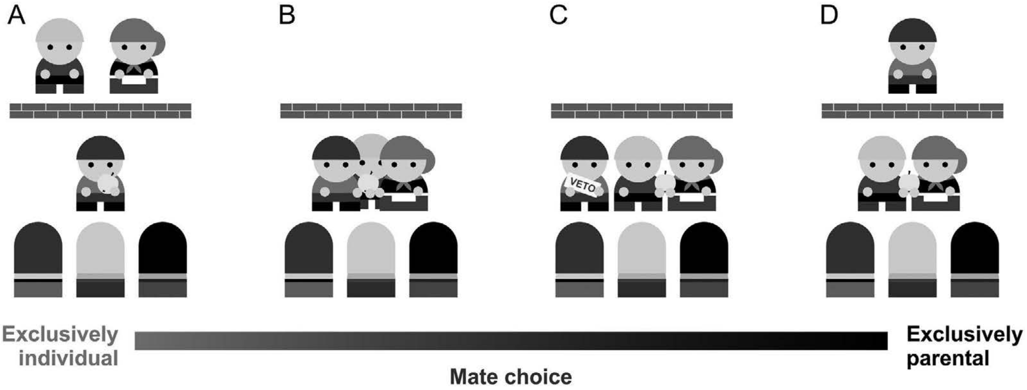

Figure 27.3 Schematic depiction of variation in parental influence on mate choice. Figures depict parents, offspring and three potential partners. Parents can (A) have no influence on their offspring's mate choice; (B) offspring and parents all contribute to the final mate choice; (C) offspring has the right of veto over parental choice; (D) offspring have no influence over mate choice arranged by parents. The power of choice is again depicted by Paris's apple. Note that the proposed typology is idealised and forms specific to various particular cultural settings need not be captured here.

characteristics, such as good health, fertility, or parenting. Preferences are also moderated by gender of the in-law: while good earning capacity is more preferred by parents in sons-in-law, characteristics such as appearance are more preferred in daughters-in-law. Due to internal fertilisation, mother – unlike father – is always certain. Moreover, women's investments in relationships are higher, which is why inappropriate mate choice has a greater impact on women and their families than on men and their kin. Parents therefore tend to interfere more into their daughters' than their sons' choice (the daughter-guarding hypothesis) and mothers tend to be more involved in their offspring's mate choice than fathers are (Apostolou 2013).

Intervention tactics

Due to differences in their preferences and expectations, the offspring and their parents often try to influence each other. Parental intervention tactics can be divided in supporting and adverse ones. Frequently used tactics include coercion (e.g. demands that the offspring behaves as the parent says), advice on whom one ought to marry, chaperoning (including going through offspring's personal belongings and seeking information about their relationships), matchmaking (e.g. buying the offspring valuable presents, such as a car, to make him/her more desirable as a prospective partner), guilt-tripping (e.g. telling the offspring that her/his relationship makes the parent very unhappy), carrot and stick (e.g. withholding/increasing allowance), social comparison, prevention, use of relatives and friends, and the famous silent treatment (not speaking to the offspring if she/he does something a parent disapproves of) (Apostolou and Papageorgi 2014). The offspring, in their turn, often employ similar tactics to influence the parents' attitudes, including advice and reasoning, guilt-tripping, coercion, persuasion, the silent treatment, social comparison, gaining trust, and threats (Apostolou et al. 2015).

Conclusions and future directions

The last three decades saw an influx of evolutionary thinking into psychology. Because mating has a direct impact on individual fitness, research on mate choice became one of the central topics in human behavioural sciences and contributed various vital insights into human mating psychology. Interestingly, this paradigmatic shift focused primarily on the adaptationist perspective and only to a smaller extent employed also the comparative and phylogenetical approach.

There is robust evidence about individual mate preferences and their variation. The main sources of individual variation include sex, age (as a proxy of reproductive potential), and mate value. A possible adaptive value seems implicitly present in most of the preferred characteristics but concrete evidence of how they contribute to fitness is often less clear. Numerous studies on preferences regarding facial masculinity and inconclusive evidence of any benefits of facial masculinity to its bearers is an excellent example (Kleisner et al. 2021). In contrast to our knowledge of mate preferences as such, our understanding of how these characteristics are integrated and translated into actual mate choice is far from complete. There is also plenty of evidence about positive assortative mating with respect to various characteristics, including age, education, ethnicity, personality, and physical appearance. The main mechanisms involve active choice of self-similar partners, by-products of competition, proximity and its effects, and convergence. While these mechanisms are not mutually exclusive, our understanding of their relative contribution is limited. Still, we believe that the main specific feature of human mate choice is the involvement of other individuals, mainly parents, which can take on many forms and levels of intensity, from light advice to fully arranged marriages. This pattern of interference seems to be unique to humans. It leads to a 'group sexual selection' and often requires a compromise among the individuals involved.

Finally, we would like to highlight the importance of cultural influences which affect human mate choice to a degree unparalleled among other species. There is evidence for population-specific

BOX 27.1 Why should comparative psychologists care about research on human mate choice?

It is often emphasised that human psychology could benefit from a comparative perspective. But is it meaningful to turn this statement the other way around? After all, humans are just one species among many. In what respects could knowledge of human psychology thus help us understand related psychological mechanisms from a broader perspective? We believe that such an endeavour could be meaningful for comparative psychology due to both ontological and methodological reasons. Firstly, all comparative psychologists so far are human, which makes research into their own species interesting and perhaps even useful in everyday settings. It also implies that they have intimate experience of human psychology and better insight into it than they can reach with respect to other species. Traditionally, behavioural researchers warn against anthropomorphising, that is, projection of human characteristics onto other species. In general we agree, but a growing body of evidence shows that some processes are shared across relatively distant taxa, such as affective mechanisms shared across vertebrates. Knowledge of humans can therefore help us gain insight into the psychology of other species if applied critically (Burghardt 1985). Secondly, in many areas of behavioural research – including research on mate preferences, sexual behaviour, and reproductive outcomes – the largest samples and richest data available are about humans. Researchers in other species can only dream about such datasets. Given this chapter's focus on human mating psychology, we limited our examples to this subject but we believe that the implications are more general.

Research on humans clearly shows that mate choice is multidimensional and this is likely to apply also to most non-human species. Emerging evidence on humans shows that integration of mate preferences may follow Euclidean, threshold, and weighted additive models (Figure 27.1). Animal research could benefit from applying these models to various non-human species. Secondly, similarly to humans, positive assortative mating was observed in numerous animal species, although the mechanisms underlying this phenomenon are unclear. Animal researchers could thus benefit from exploring individual mechanisms proposed for humans (Figure 27.2). Thirdly, while we suggested that parental influence in mate choice is specific to humans (Figure 27.3), similar patterns in other species may be just awaiting their discovery. Suitable candidates could be species with intergenerational inheritance of, for instance, dominance rank, territory, or nesting places. Finally, studies on humans show that parental characteristics may serve as a template for mate preferences of their offspring but these processes do not meet the requirements of classical imprinting, such as restricted exposition, sensitive period, and irreversibility. It is possible that in other species, these canalised learning processes are thus more flexible than previously expected as well.

mate preferences shaped by social learning in other species, such as songbirds and whales (Noad et al. 2000). In humans, however, the variation in all aspects of mating is, due to cultural diversity, enormous. It leads to a vast range of mate preferences for body modifications, courtship practices, formation of mating unions (marriage), regulations on how and when these unions can be dissolved, who can enter the union (i.e. mating systems), resource transfers related to union formation (dowry and bride price), and a lot more (Hamon and Ingoldsby 2003). This clearly shows that by excluding cultural practices from behavioural analyses, scientists would miss a large part of human variation. We do not advocate an exclusively proximate approach, which is what many social scientists would propose. We are confident that the evolutionary framework is a heuristic approach to human mating fully capable of taking into consideration processes of both biological and cultural evolution as well as their interactions.

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28

BRIDGING THE GAP

Human-animal comparisons

Katherine McAuliffe and Paul Deutchman

Introduction

A common sight in presentations and publications about comparative cognition is a branching phylogenetic tree showing us—*Homo sapiens*—at the tip of one of the long branches, flanked by our primate cousins, chimpanzees, bonobos and gorillas. More ambitious depictions place humans at the tip of a bigger tree, one that encompasses a breadth of other taxa, including non-primate mammals, birds, fish and even invertebrates. These depictions imply that value can be derived from comparing humans to other species and, more specifically in the context of comparative cognition, that comparing human cognition to the cognition of other animals is a worthwhile endeavor. While this is undoubtedly true, it is important to consider what we can and cannot learn from these human-animal comparisons. What can these comparisons teach us about the parts of human cognition that are shared with other species and those that are more specific to our species, as well as the selective forces that shape cognitive solutions to social and ecological problems more generally?

In this chapter we tackle these questions by first reviewing two *kinds* of approaches commonly employed by researchers who wish to compare cognition in humans and other species. Our first section focuses on *methodological approaches* wherein a particular paradigm designed to test humans is used to test other animals (down-linkage) or vice versa (up-linkage). We focus on studies of inequity aversion in humans and other animals as a domain of research that illustrates the utility of employing a common methodology across different species. Our next section focuses on two different *motivations* for studying animal cognition, one that places a greater focus on the question of where a particular cognitive capacity or behaviour comes from (herein labelled the "top-down" approach), often asking either whether a feature of human cognition is unique to humans or shared with other species. The other places a greater focus on understanding how particular ecological and social problems shape the evolution of similar cognitive solutions across species (herein labelled the "bottom-up" approach). In this second section, we focus on studies of punishment in humans and other animals as an area of study that fruitfully illustrates the utility of both the top-down and bottom-up approaches. We end by highlighting insights that can be generated through these kinds of comparisons and by making suggestions for future work.

We wish to note that, as researchers ourselves, our principal interest lies in the evolution and development of cooperation. Thus, most of the examples we draw from focus on behaviours and cognitive abilities related to cooperation. However, the major themes we cover here do not apply specifically to cooperative cognition but rather apply broadly to research that compares the cognition of humans and other animals.

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Methodological approaches: down-linkage and up-linkage

From a methodological perspective, work comparing humans to other species can be organized into two broad categories depending on the direction of comparisons (Figure 28.1). The first category consists of studies that start with a task designed for human research, and subsequently adapting the paradigm for animal testing. Methodological adaptations in this direction are known as *down-linkage* studies (Smith & Silberberg, 2010), a term which we use here for consistency with existing literature and notably not because we agree with the implied taxonomic hierarchy. For instance, Lakshminarayanan and colleagues (2011) adapted Tversky and Kahneman's original framing effect study (1981)

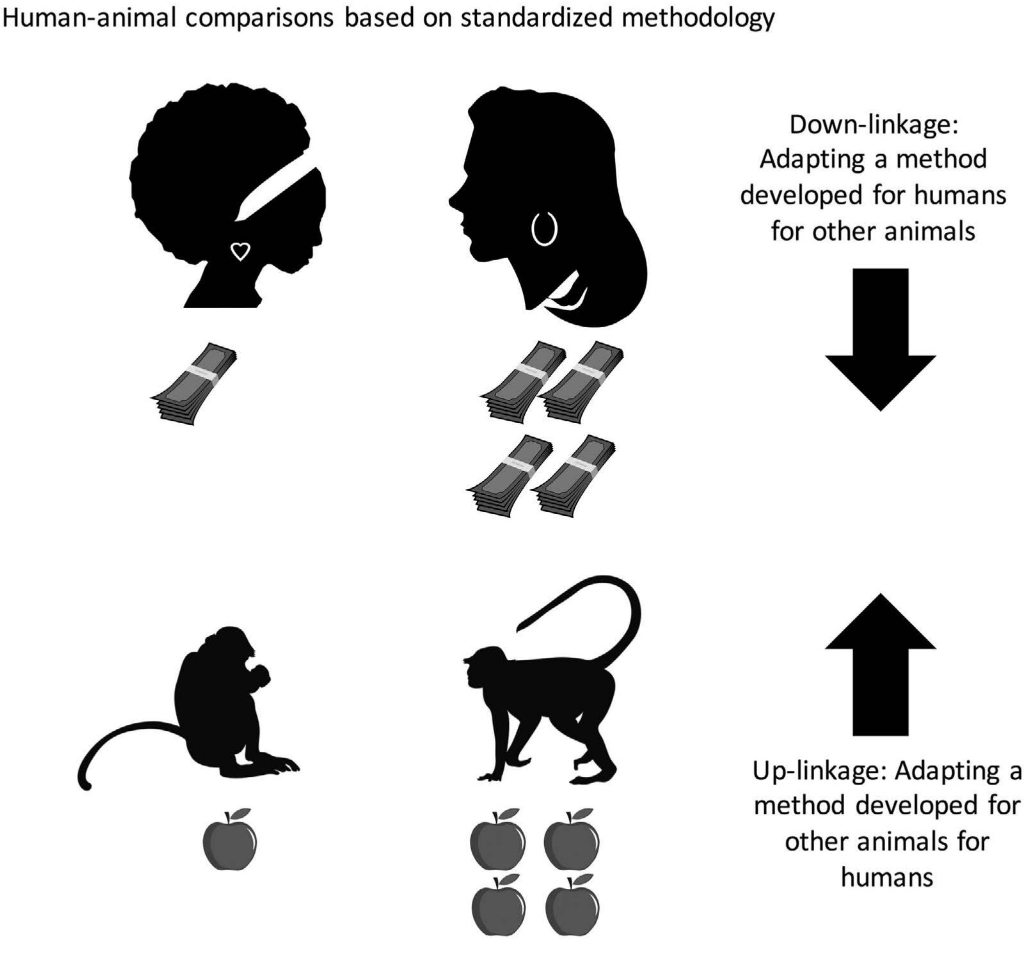

Figure 28.1 Diagram illustrating down- and up-linkage studies. In these studies a common methodology is employed across participant categories (e.g., humans and nonhuman primates). Standardizing the methodological approach can help facilitate human-animal comparisons by generating responses that can be compared directly. The example above illustrates paradigms developed to test participants' aversion to unequal resource distributions. Human participants are typically presented with distributions of money (represented here by cash) while nonhuman primate participants are typically presented with distributions of food (represented here by apples). Participants' responses to unequal (depicted) versus equal (not depicted) distributions are elicited and the strength of these responses is then compared across species.

Images from pixbay.com.

and found that brown capuchin monkeys (*Sapajus [Cebus] apella*) exhibit a similar pattern of risk preference to humans: they are risk-seeking when decisions are framed as a loss and risk-averse when they are framed as a gain. Lakshminarayanan and colleagues' study nicely highlights how researchers can adapt tasks originally conducted on humans to address similar questions in other species, sometimes finding a surprising degree of similarity in behaviour between species. Methodological adaptations in the other direction—cases in which a task originally designed to study other species is adapted for humans—are known as *up-linkage* studies (Smith & Silberberg, 2010). For instance, Inoue and Matsuzawa (2007) compared the working memory ability of humans to chimpanzees using a limited-hold memory task, a task in which participants had a fraction of a second to memorize the position of numbers on a screen before they were masked with white squares and then had to touch the squares in the correct order. Three different hold duration conditions were tested: 650, 430 and 210 milliseconds. This task was originally designed to test memory in chimpanzees and was then used to test human participants, illustrating adaptations in the up-linkage direction. They found that humans and adult chimpanzees were roughly equivalent in the task whereas younger chimpanzees outperformed human adults on the faster trials. Both of these examples illustrate a major benefit of adaptations in both down- and up-linkage directions: namely, they offer a degree of methodological standardization that helps facilitate human-animal comparisons because participants' responses are captured in the same (or, at least, very similar) way.

A case study: inequity aversion in humans and animals

Studies of inequity aversion provide an illustrative example of the utility of up- and down-linkage tasks in drawing comparisons between humans and other species. The term inequity aversion refers to an aversion to unequal resource distributions (note that in this chapter we use the terms inequity and inequality interchangeably, though these terms can have slightly different meanings with 'inequality' referring specifically to unequal distributions and 'inequity' referring to unfairness that depends on contextual factors such as merit and need). This aversion can exist in one of two directions: *disadvantageous inequity aversion*, an aversion to receiving *less* than others, and *advantageous inequity aversion*, an aversion to receiving *more* than others. A wealth of theoretical and empirical work suggests that inequity aversion is an important part of human cooperative cognition (Fehr & Schmidt, 1999; Dawes et al., 2007, Lowenstein, Thompson & Bazerman, 1989) and is core to the human sense of fairness (McAuliffe et al., 2017). Moreover, inequity may serve an important role in cooperative interactions (Fehr & Schmidt, 1999; Brosnan, 2011), perhaps by helping cooperative agents avoid exploitation by those who freeride the cooperative effort of others, and by encouraging individuals to seek mutually beneficial cooperative partnerships.

The first study to ask whether animals share an aversion to unequal resource distributions was conducted by Brosnan and de Waal nearly two decades ago (Brosnan & de Waal, 2003). In this study, brown capuchin monkey subjects were paired with a partner and both subject and partner were offered the chance to exchange tokens for food rewards with an experimenter. In the equal condition, both subject and partner received a low quality food item (cucumber). In the inequity condition, one subject received the low quality food item for trade while their partner received a higher quality food item (grape). Thus, in this condition the monkeys received unequal pay for trading the same token. The measure of interest was whether the subjects would accept or reject the 'unfair' deal—i.e., would they complete the exchange in the inequity condition or refuse? Capuchin monkeys were less likely to exchange in the inequity condition compared to the equal condition, a finding interpreted as evidence of inequity aversion. While findings from Brosnan & de Waal's paper are certainly intriguing, it is important to note that the study's conclusions were controversial (Henrich, 2004b; Wynne 2004; see below for more detail) and evidence for inequity aversion in nonhuman primates has since received mixed support (e.g., Brosnan et al., 2010; Bräuer et al. 2006; McAuliffe et al., 2015). Nevertheless, this study introduced an inequity aversion paradigm for nonhuman animals that catalyzed a wave of work on inequity aversion in primates and other species and, most importantly for our purposes, that sets the stage for a productive discussion of down- and up-linkage studies.

The task that Brosnan and de Waal designed is based on economic games commonly used with humans to study responses to unfairness. While not a direct replication of any one task, it roughly maps on to the Ultimatum Game (Güth et al., 1982), a game in which a proposer can offer a split of resources to a responder and the responder can in turn accept or reject the split. The Ultimatum Game has been used widely in studies of fairness and punishment with adults across many different countries (Henrich et al, 2005; Oosterbeek et al., 2004), and results show that people across societies propose and reject more than would be expected by utility maximization alone (e.g., Henrich et al., 2005); that is, people reject nonzero splits even though (from a purely self-interested perspective), receiving something is better than receiving nothing. Rejections in this context meet the definition of inequity aversion (n.b., they also meet the definition for punishment; see Section 3 for details), raising the question: can we compare results from the token exchange paradigm to results from the Ultimatum Game?

One key difference between the token inequity aversion paradigm and the Ultimatum Game is that, in the Ultimatum Game, the responders' decisions influence the payoffs of both players, whereas in the token exchange paradigm the subjects' responses affect only their own payoffs (i.e., the partner gets the grape regardless of whether the subject completes or refuses the exchange; see Henrich, 2004b and McAuliffe & Santos, 2018 for a discussion of why this matters).[1] Additionally, in the token exchange paradigm, the allocations come from a third-party (the experimenter), making it a three-player game (see Engelmann et al., 2017 for a discussion of the role of the experimenter in these tasks), whereas in the Ultimatum Game one player offers the splits, making it a two-person game. Thus, while there are clear parallels between tasks designed to measure inequity aversion in monkeys and humans, there are also differences that make data from these tasks difficult to compare directly.

In response to the difficulties associated with directly comparing inequity aversion in humans and animals, researchers have sought to more closely match experimental paradigms used for animals and humans. For instance, two research groups designed 'up-linkage' versions of the token exchange paradigm to test whether adult human participants would respond in the same way as capuchin monkeys to unequal payoffs in a task that closely mirrored the token exchange paradigm (Ostojic & Clayton, 2013; Hachiga et al., 2009). Ostojic and Clayton (2013) designed a task in which participants were paired up and had to complete "work" by pressing a pump within a given time frame in order to receive a reward from a third party. Depending on the experimental condition, participants were presented with trials in which they had to press the pump for either an unequal (1–6; i.e., 1 for the participant, 6 for the partner) or equal (1–1) reward distribution to both players. They found evidence in support of inequity aversion in humans: participants completed less work when the reward was unequal as compared to equal. These studies showcase the utility of adapting a task designed for animals and testing humans using the same—or, at least, very similar—methodology. In this case, for example, this direct comparison helped draw a clear connection between inequity aversion as measured in animals and inequity aversion as measured in humans.

Work from our team has similarly sought to closely match inequity aversion paradigms between humans and animals, this time in the down-linkage direction. Inspired by economic paradigms like the Ultimatum Game, Blake and McAuliffe (2011) designed an intuitive economic game for children which was designed to measure when, in development, children begin to reject unequal resource allocations. In this game, two children are recruited to play a face-to-face game using a child-friendly wooden apparatus (Figure 28.2). One child is assigned to the role of actor (akin to the "subject" in the token exchange paradigm or the "responder" in the Ultimatum Game) while the other is assigned to the role of recipient. As in the token exchange paradigm designed for capuchin monkeys, an experimenter allocates resources, in this case candies, between the two children. Allocations are either equal—one candy for each child—or unequal. Unequal allocations vary in their

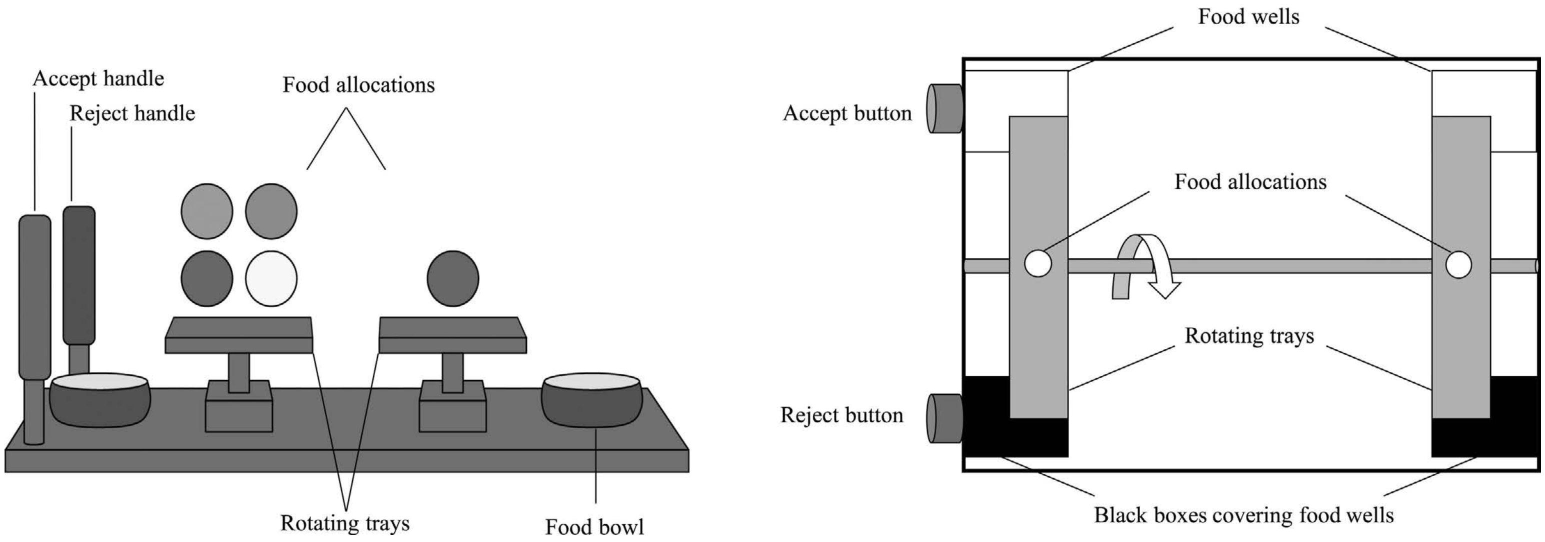

Figure 28.2 Apparatus used to test inequity aversion in children (left) and capuchin monkeys (right). In both set-ups, participants have the opportunity to accept or reject allocations. Their behaviour affects the distribution of food to both actors—the individuals in charge of the handles/buttons—as well as their partners. Note that colors were added to the diagram of the capuchin apparatus to illustrate parallels with the child apparatus: in reality the buttons were black.

directionality. In the *disadvantageous* condition, the actor gets less than their peer, receiving one candy while the recipient receives four. In the advantageous condition, the actor receives more than their peer, receiving four candies while the recipient receives one. The actor can accept allocations by pulling the green handle, which causes the trays to tip outward, thereby delivering the candies to the two children's bowls. Alternatively, the actor can reject allocations by pulling the red handle, which causes the trays to tip inward, thereby delivering candies to a middle bowl which belongs to neither child. A decade of work using this paradigm has shown that young children across societies reject disadvantageous allocations, showing a foundational aversion to receiving less than others (Blake & McAuliffe, 2011; Blake et al., 2015; McAuliffe et al., 2017), whereas only older children in some societies reject advantageous allocations, showing a more flexible aversion to receiving more than others (Blake et al., 2015).

A strength of the Inequity Game paradigm is that it shares key features with the Ultimatum Game in that both players' payoffs are contingent on the actor's decision. However, because payoffs are contingent in this task but not contingent in typical animal paradigms, it is difficult to compare children's responses to inequality in this game to animals' responses in token exchange paradigms. To facilitate human-animal comparisons of inequity aversion, members of our team built on the Inequity Game designed for children to test inequity aversion in an analogous task across several species including cotton-top tamarins (*Saguinus oedipus*; McAuliffe et al., 2014), cleaner fish (*Labroides dimidiatus*; Raihani et al., 2012) and brown capuchin monkeys (McAuliffe et al., 2015; this is the same species of capuchin monkey tested in Brosnan and de Waal's original task). Across these tasks, one subject is in a position to accept equal versus unequal payoff distributions. However, from there, the precise methods differ depending on the species being tested. For instance, in our study of cotton-top tamarins (McAuliffe et al., 2014), subjects could pull a tool that would deliver a small tray of food to them and to their partner, creating a situation that closely mimicked the child experiment described above. Our measure of interest was whether subjects' decisions to pull (i.e., accept) versus not pull (i.e., reject) were predicted by the allocation of rewards on offer and, more specifically, whether the allocation was equal or unequal. In our study of cleaner fish (Raihani et al., 2012), a small reef-dwelling fish known for cooperating in pairs to clean client fish (Bshary, Gingins, & Vail, 2014; Côté, 2000; Grutter & Bshary, 2003), cleaner subjects were given the opportunity to provide tactile stimulation to a plexiglass plate. Once tactile stimulation had been delivered, a second plate was delivered, which contained either an equal allocation of rewards between the subject and partner, or an unequal allocation. In this study, our measure of interest was how long it took subjects to provide tactile stimulation. We reasoned that if cleaner fish are averse to inequality, subjects should take longer—showing less motivation—when the payoffs were unequal. McAuliffe (in revision) used a similar design to Raihani et al. (2012) to study inequity aversion in domestic dogs (*Canis familiaris*) and dingoes (*Canis dingo*), wherein motivation was measured by willingness to approach a food plate rather than latency to provide tactile stimulation. Findings from both the cleaner fish and dog/dingo inequity aversion tasks suggested that motivation was not affected by unequal reward distribution, providing no evidence for inequity aversion in these species.

The most direct comparison between the child and animal version of the inequity game was the game designed for capuchin monkeys. For this task, we designed a version of the Inequity Game apparatus that would be appropriate for testing with capuchin monkeys. While these adaptations required some changes, such as using buttons as opposed to levers and changing the food rewards, we successfully retained the core features of the task. Namely, subjects could accept allocations through one action—pushing a green button that would deliver rewards to themselves and a partner—and could reject allocations through another—pushing a red button that would deliver rewards to boxes that were inaccessible to both monkeys (Figire 28.2).

Critically, like the child study and unlike most other work on inequity aversion in nonhuman animals, we tested both disadvantageous and advantageous inequity aversion (although note that in our study of capuchins, inequity was operationalized as inequities of food quality as opposed to food quantity). Capuchins in our task were no more likely to reject unequal payoffs—in either the disadvantageous or advantageous directions—than equal payoffs (McAuliffe et al., 2015). This result stands in contrast to the findings of Brosnan & de Waal (2003) and the possible reasons for this difference are discussed in McAuliffe et al (2015). Regardless, this study provided a useful contribution to the growing literature on inequity aversion because it operationalized participants' behaviour identically to the human study by asking whether participants wished to accept or reject in a task that affects both their payoff as well as their partner's. From this comparison, we inferred that while children show an early-emerging aversion to disadvantageous inequity, one which grows stronger with age, we do not see a similar response in capuchin monkeys. Because this offers one of the cleanest comparisons of inequity aversion between humans and nonhuman animals, we believe it raises important questions about whether the hallmark for inequity aversion in animals is the same kind of response that we consider to be inequity aversion in children (see McAuliffe & Santos 2018 for a discussion). Of course, it is worth noting that this work compares adult monkeys to juvenile humans, and it is important that inferences about cross-species comparisons be constrained accordingly (please see Box 28.1: Comparative Developmental Psychology).

Box 28.1 Comparative Developmental Psychology

Work comparing cognition in humans and animals often compares evidence from the adults of one species to the juveniles of another. For instance, a great deal of work has examined cognitive abilities of humans relative to apes by comparing children's performance on a given task to the performance of adult chimpanzees, bonobos and orangutans (Pongo pygmaeus) (e.g., Nagell et al., 1993; Warneken et al., 2006; Warneken & Tomasello, 2006). These comparisons have been informative in shaping our understanding of which aspects of human cognition are relatively sophisticated early in development, for instance showing that young humans outperform our ape cousins on social but not physical cognition tasks (Herrmann et al., 2007). However, it is important to consider how the developmental trajectories of different cognitive abilities may affect and importantly constrain human-animal comparisons.

Researchers have begun to highlight the importance of this developmental comparative approach to studying the ways in which human cognitive development is similar or different to other animals (Rosati et al., 2014). This approach is informative because it can shed light on how the pacing and pattern of human development compares to other species. For instance, Wobber et al. (2014) compared 2- to 4-year-old children and similarly-aged chimpanzees and bonobos on a range of cognitive tasks assessing physical and social cognition. They found that at 2 years of age, children already outperformed apes in the same age range at skills of social cognition, and that this difference increased throughout development. Interestingly, patterns of development between humans and apes differed more in the social domain than the physical domain, suggesting that one of the key differences between humans and other animals is our social cognitive abilities. By comparing cognitive development between species, Wobber and colleagues (2014) were able not just to show that children outperform apes in social cognition tasks, but that this advantage for humans is present very early in development and social-cognitive abilities emerge faster in human ontogeny than ape ontogeny. In sum, comparative developmental psychology offers an important approach for studying comparative cognition, one that offers great promise for testing theories of human development (Rosati et al., 2014).

Summary

The examples raised above highlight the utility of standardizing methodological approaches in animal and human tasks. We reviewed examples that showcase how tasks can be adapted from animals to humans (up-linkage) and from humans to animals (down-linkage). These adaptations facilitate comparisons across categories of participants, principally because behaviours are operationalized in the same way. Of course, standardization has its limits: a study for humans and a study for fish will obviously differ in some ways. However, in seeking to investigate cognition and behaviour using a common currency—for instance, willingness to accept unequal payoffs—we can begin to paint a picture of the taxonomic distribution of different cognitive abilities, which in turn can provide insight into when they evolved and the selective pressures that shaped them. For instance, if we were to see inequity aversion only in obligate cooperative breeders, this would provide evidence consistent with there being an important relationship between inequity aversion and cooperation. Or, if we were to see inequity aversion only in apes and not in other species, this would provide evidence that inequity aversion likely arose around the time of the last common ancestor of extant apes. To be clear: neither of these patterns is actually supported by existing data, but we raise them here to make concrete the *kinds* of inferences that can be drawn from studies conducted using standardized methodologies across diverse taxa.

Motivated approaches: bottom-up and top-down approaches to studying cognition in humans and other species

One main motivation for comparing human cognition to those of other animals is to understand which aspects of our psychology are unique to humans. To this end, a common approach is to consider a phenomenon known to be important to humans and to test whether other species show any evidence for it. This kind of approach, one that starts with the psychological trait of interest and looks for its expression in other species, can be considered a top-down approach. The label "top-down" refers to the idea that the starting point is a mental process. An alternative approach is to first consider the ecological constraints present in different species and to ask how different cognitive abilities evolved to solve particular ecological or social problems. This approach can be considered a "bottom-up" approach in that it starts with the problems that must be solved and then examines candidate psychological mechanisms that may help organisms solve those problems (related to but not identical to "bottom-up" *sensu* Shettleworth, 2009).

The many studies that have explored analogs of language in animals provide a nice illustration of top-down comparisons. Language is one of the defining features of our species and a question that remains hotly debated is whether other species show the signatures of human language such as syntax, semantics and phonology (For deeper discussions of these issues see, for example, Bolhuis et al., 2014; Townsend et al., 2018; Engesser & Townsend, 2019 as well as Chapter 20). Famous examples exist of individuals across diverse species, such as Alex, an African gray parrot (*Psittacus erithacus*), and Kanzi a bonobo (*Pan paniscus*), who had the capacity to communicate with humans using English words. Although these individuals do not necessarily provide insight into species-typical abilities (Thornton & Lukas, 2012), they nevertheless showed what was *possible* in terms of the language abilities of other species, shedding light on which features of human language are more versus less shared with members of other taxa. Another example, and one that does not rely on extensive human input as was the case with Kanzi and Alex, comes from the exploration of syntax in nonhuman animals. The use of syntactic structure is key to human's language ability and researchers have examined whether nonhuman animal communication is syntactical. Townsend et al (2018) explored this question, finding that call combinations in male Campbell's monkeys and pied babblers show some similarities to nonproductive, nonhierarchical syntax in human language. These top-down studies have been helpful in shedding light on the selective forces that shape communication across species, including human language.

Work on teaching in nonhuman animals (Thornton & Raihani, 2008) provides an example of bottom-up comparisons. For instance, meerkat (*Suricata suricatta*) adults teach young pups in their groups to feed on mobile and sometimes dangerous prey items such as scorpions (Thornton & McAuliffe, 2006). Adults gradually introduce pups to these prey items: pups are initially fed dead scorpions, then, disabled scorpions and, just prior to foraging independence, fully intact scorpions. In doing so, adults help scaffold prey handling abilities in pups, a behaviour which meets the functional definition of teaching (Caro & Hauser, 1992). Moreover, the mechanisms supporting this behaviour are relatively simple: helpers base their provisioning behaviour on pups' begging calls, which change as pups grow. This work is interesting in the context of bottom-up approaches to comparative cognition because it illustrates a context in which an apparently sophisticated behaviour can be shaped by ecological pressures and based on simple cognitive mechanisms. Moreover, work of this kind can have implications for our understanding of human behaviour and cognition: indeed, work on the evolution of teaching in animals has informed theoretical and empirical work on human teaching (Kline 2015; Lucas et al., 2020).

In the case study discussed below, we examine bottom-up and top-down approaches within a single category of behaviour: punishment. This body of work illustrates the value of both approaches and highlights the human-animal comparisons that result from them. Before diving into this case study, however, we wish to note that these approaches need not be entirely mutually exclusive. Rather, they represent a helpful way to organize existing work that compares the psychology of humans and other species. Additionally, these different motivations for studying animal work and the human-animal comparisons that can arise from them are not distinct from the down- and up-linkage methodological approaches reviewed in Section 2. Indeed, these two ways of categorizing human-animal comparisons are in some ways orthogonal to each other: Comparative cognition research born of both top-down and bottom-up motivations may generate human-animal comparisons that result in down- and up-linkage studies.

A case study: punishment in humans and animals

Costly punishment (hereafter 'punishment') can be defined as a behaviour in which the punisher pays a cost in order to inflict a cost on a partner (Clutton-Brock & Parker, 1995). Punishment has been widely studied across disciplines and is known to be a foundational mechanism of behaviour modification (for reviews see Raihani, Thornton & Bshary, 2012 and Seymour, Singer & Dolan, 2007; Raihani & Bshary, 2019). In the context of cooperation, punishment is known to play an important role in encouraging costly prosocial behaviour (Boyd et al., 2010; Boyd & Richerson, 1992; Fehr & Fischbacher, 2004) and maintaining cooperation over time (Balliet et al., 2011; Fehr & Fischbacher 2003; Fehr and Gächter 2002). Indeed, punishment is thought to have played an important role in the evolution of cooperation in humans (Boyd, Gintis, Bowles, & Richerson, 2003; Boyd & Richerson, 1992; Henrich & Boyd, 2001, but see Guala, 2012). Humans punish uncooperative partners in both second-party contexts, in which the punisher is directly harmed by the transgressor (Fehr & Gächter, 2000; Güth et al., 1982; Bone & Raihani, 2015), and third-party contexts, in which the punisher is an uninvolved observer (Fehr & Fischbacher, 2004).

Studies examining punishment in cooperative animal species are often structured in ways that are broadly consistent with what we have described above as a bottom-up approach. Specifically, these studies bring empirical evidence to bear on the question of what kinds of cooperative problems punishment can solve in the wild. Yet, a major take-home from this work is that punishment is not especially common in cooperative systems outside of humans (Riehl & Frederickson, 2016). Punishment that occurs within systems of cleaner fish and their clients, which we describe next, may thus represent a particularly valuable context in which to explore punishment in cooperative animal societies.

In our view, the punishment that occurs between cleaner fish and their client fish in the cleaner-client mutualism offers one of the clearest glimpses into the kind of cooperative problems that

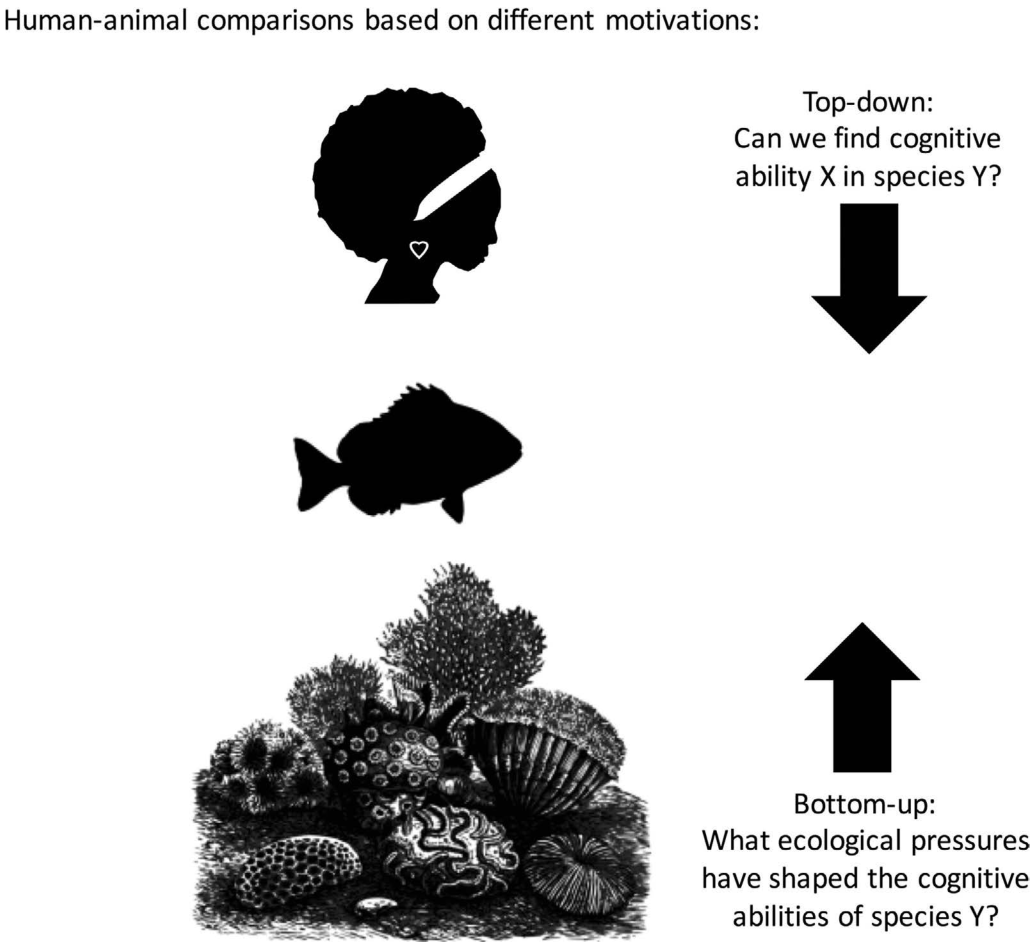

Figure 28.3 Diagram illustrating two different motivations for studying cognition in animals. In the top-down direction, researchers are often interested in identifying a cognitive ability of interest, commonly an ability known to be important to humans, and asking whether other species show signs of sharing the target ability. In the bottom-up direction, researchers explore how the cognitive abilities of individuals in a given species have been shaped by ecological and social pressures.

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punishment can help solve in nonhuman animals. In this system, cleaners work together or alone to remove ectoparasites from client fish. Cleaning offers mutualistic benefits: the cleaners get a meal and the clients get cleaned. However, the system also represents a cooperative dilemma because cleaner fish prefer to eat mucus from the clients over ectoparasites, a behaviour which is detrimental to the client fish and which, in some cases, prompts clients to aggressively chase cheating cleaners, a behaviour that meets the definition of punishment (Bshary & Grutter, 2002). This cooperative dilemma becomes even more complex (and even more interesting!) when two cleaners work together to clean a client. In these cases, a cheat can spoil the mutualistic interaction not only for themselves but also for their cleaning partner. Here, punishment offers a solution. When dyads are working together to clean a client, a cheat is sometimes punished (i.e., aggressively chased) by their partner. Critically, experiencing punishment makes cheats more likely to cooperate in future interactions (Raihani et al., 2010). This finding shows intriguing parallels with research on humans which has that found punishment promotes cooperation (e.g., Fehr & Gächter, 2002). However, it is important to note that in the cleaner fish system, punishers benefit directly from their punishment, which is not the case in some paradigms used to study human punishment (e.g., Fehr & Gächter, 2002).

Top-down research on animal punishment asks what features of human punishment are shared with other species, and which are unique to humans. For example, one well established feature of punitive behaviour in humans is that punishment is sensitive not only to the outcome of a transgressor's behaviour but also to the intent that drove that outcome. For instance, when the transgressor intended to cause the outcome, they are judged as more blameworthy and punished more severely than if they unintentionally caused the same outcome (Cushman, 2008; Greene et al., 2009).

One particularly useful way of capturing sensitivity to intent is through constraining individuals' choices. This approach has been applied to understanding when adults punish unfair behaviour. For instance, in the mini Ultimatum Game, a variation on the Ultimatum Game we described in Section 2, proposers choose between two preset allocations (e.g., 50/50 split versus 80/20 split). Responders are aware of the proposer's choice set and, as in the standard game, can accept or reject the choice. Work using this paradigm has shown that people take into account the proposer's choice set. For instance, responders are more likely to reject an 80/20 split (proposer keeps 80% of the endowment and offers 20%) if the proposer had a 50/50 split as an alternative option. That responders take into account a proposer's outside options suggests that responders use information about what choices proposers *could have* made to provide information about the proposer's intent. Indeed, consistent with this interpretation, responders are more likely to accept an 80/20 split when the proposer had no other option or an even more selfish option (e.g., 100/0 split; Sutter et al., 2007). Thus, work with humans suggests that punishment is sensitive to more than just outcomes: it also sensitive to information about the perpetrator's intent.

The fact that humans integrate information about intent, and factor in outside options in making punishment decisions raises the question of whether any other species do this as well. Studies that have tackled this question can help illustrate punishment research motivated by a top-down approach. Two examples are particularly illustrative. The first is a study by Jensen and colleagues (2007a; later replicated by Riedl et al., 2012) that presented chimpanzees with a scenario in which one individual (the victim) had access to a table with food on it. Another individual, the partner, had access to a rope that could be used to steal the food from the victim, pulling it over to their own enclosure. The victim then had the opportunity to pull a different rope that would collapse the table, causing all food to fall out of reach. A key comparison was how likely victims were to collapse the table—the punishment measurement—when the partner stole their food by removing the table (i.e., negative outcome with negative intention) compared to when an experimenter pulled the table away from the victim and toward the partner (i.e., negative outcome with no negative intention). Results showed that punishment was more common when the partner stole the table, suggesting the chimpanzees reciprocate losses but are not spiteful—i.e., they were not inclined to punish the partner when they had not intentionally stolen, even when the food had been removed by an experimenter. This provides initial evidence that at least one nonhuman species bases punishment decisions on more than outcomes alone. Work with chimpanzees that more closely parallels the mini Ultimatum Game suggests that responders do not factor information about proposers' choices into their rejection behaviour (Jensen et al., 2007b). However, it is important to note that chimpanzees rarely reject in the Ultimatum Game (Jensen et al., 2007b; Proctor et al., 2013), meaning that the Ultimatum Game is probably not the ideal context in which to explore their sensitivity to outside options.

Cleaner fish present an excellent model in which to study factors supporting punishment outside of humans (Raihani & McAuliffe, 2012). Together with our collaborators, we tested whether cleaner fish are sensitive to their partner's outside options when deciding whether or not to punish (Deutchman et al., in prep). This study was borne of a top-down motivation to understand whether a feature common to human punishment—sensitivity to intent—can be found in a nonhuman animal. We designed a task to compare punishment in a condition in which individuals chose to cheat, to one in which individuals had no choice but to cheat. More concretely, we presented females in female-male dyads with 'choice' trials: they could eat less preferred fish food flakes—a stand-in for ectoparasites on client fish and representing a cooperative behaviour, or they could eat more preferred prawn items—a stand-in for client fish mucus, representing a cheating behaviour. As with cheating in the wild, if cleaners ate the prawn item the plate was removed from the water, representing the client fish ending the relationship. Their partner, the male, would watch them feed and then had the opportunity to punish. We compared punishment in this condition to one in which the females were presented *only* with prawn items: i.e., they had no choice but to cheat. Although males did engage in punishment, we found no difference in males' punishment between these conditions, indicating that they did not factor females' outside options into their punishment decisions. When we ran an up-linkage version of this study with human adults in an economic game played online, we found that outside options did matter and that they mattered in the predicted direction: namely, adults were more likely to punish those who chose to cheat than those who had no choice (Deutchman et al., in prep). Thus, based on existing comparative evidence testing chimpanzees and fish, it does not seem as though information about cheaters' outside options influences punishment behaviour like it does in humans.

Summary

Bottom-up studies of animal cognition ask how ecological and social pressures have shaped cognitive abilities. While these studies do not *require* human-animal comparisons, they often lead to them and, in doing so, help us better understand how different problems can lead to the same cognitive solutions (e.g., teaching in meerkats and punishment of cheats in cleaner fish). Top-down studies of animal cognition, on the other hand, typically include either direct or indirect human-animal comparisons because they originate in a question about whether a given cognitive ability—commonly one identified in humans—is observed in other species (e.g., language and intent-based punishment in animals). Together, studies in both bottom-up and top-down directions can help shed light on the selective forces that shape cognition in humans and other species.

Conclusion

In this chapter, we have reviewed two major categories of *kinds* of approaches commonly employed by researchers who wish to compare cognition in humans and other species. We first examined down- and up-linkage studies to show how methodological standardization can help facilitate human-animal comparisons. We reviewed studies of inequity aversion in animals to highlight these comparisons in both down- and up-linkage directions. We then examined bottom-up and top-down studies to show how different motivations for studying animal cognition can lead to, and may even require, comparisons with humans. Under this second section, we focused principally on studies of punishment in nonhuman animals, focusing on punishment in cleaner fish. We did so because, in our view, these studies nicely illustrate the utility of studying cognition in species that face dramatically different ecological pressures when compared to humans.

In concluding, we wish to return to the picture we painted in the introduction of this chapter: one of a phylogenetic tree that shows humans at the tip of one of its many reaching branches. We hope that this chapter has conveyed the value of studying cognition in humans as well as other animals in a broadly comparative context. We can only learn so much about why minds are the way they are by studying any single species in isolation. Through thoughtful comparative designs, we can better understand the features of human cognition that are more versus less shared across other taxa. Moreover, through cross-species comparisons that include—but are not limited to—human-animal comparisons, we can bring the selective forces that shape cognitive solutions to social and ecological problems into sharper focus.

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Note

1. Note that this feature of the game makes it more similar to a less widely-used game called the Impunity Game (Yamagishi et al., 2009), in which proposers offer a split to responders but, regardless of whether responders accept or reject, proposers keep the proportion that they allocated to themselves.

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