Introduction. The Concept of Umwelt in Experimental Animal Cognition

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Yes, the ant says again,
I've seen the stars (. . .)
The snail asks:
But, what are stars?
They're lights we carry
Over our heads.
We can't see them,
The ants say.
(. . .)
We'll kill you, you're
Lazy and perverse.
The Encounters of an Adventurous Snail
(Federico García Lorca, 1918)

Living in the world mostly consists of receiving perceptual information and performing actions according to this information. This combination of what we can perceive ('Merkwelt') and what we can do ('Wirkwelt') was defined as 'Umwelt' by Jakob Johann von Uexküll (1934/2010). According to Uexküll, the concept of Umwelt comprises the extent of every being's existence: there is no more external information than what we can perceive through our senses, and there is no more capacity of action than what we can actually do with our anatomy. Indeed, imagining the world with a different perspective from the one we daily live in is particularly challenging. Although all individuals and species live in the same objective reality (Kant's 'noumenon': Kant, 1781/1998), perceptual limitations only allow species to perceive part of this reality ('phenomenon') through their senses. Species' (and individuals') reality is therefore subjective and limited by their perceptual and factional characteristics – their Umwelt. In Uexküll's (1920/2014, pp. 92–93) words: 'The real thing is that there is no real world but as many worlds as species – and individuals'.

As humans, we are no exception to this rule: our perception of reality is also limited by our Umwelt, and it is no easy task for us to put ourselves in other animals' shoes. This limitation is especially relevant for comparative psychologists, ethologists and researchers interested in animal cognition. First, understanding the different Umwelt of other species is necessary to come up with socio-ecologically relevant tests of cognition and avoid anthropocentrism. Although interspecific comparisons can be highly informative on the evolution of human cognition (i.e. which specific cognitive skills are uniquely human, and why), studying cognition in species other than humans is also

highly rewarding per se. In this respect, behavioural observations can tell us a lot about the socio-ecological challenges that different animals face in their everyday life, and on the cognitive skills that may be linked to these challenges, which can be very different from our own. As Ramón y Cajal (1897/2016) noted, 'our appreciation of what is important and what is accessory; what is big and what is small; lie on a false judgment, namely a truly anthropomorphic error'.

Second, considering the species' merkwelt is essential to design experimental set-ups best framed to the species' perceptual systems. Some species, for instance, rely on different senses (e.g. electroreception) or perceive stimuli with different thresholds (e.g. infrared light). Failing to take this into account may not only lead researchers to use stimuli with little relevance for the study species (e.g. colour stimuli that cannot be easily discriminated in a learning task), but also to inadvertently provide cues to the study subjects (e.g. odour cues when testing object permanence in species largely relying on olfaction).

Third, taking into account the species' wirkwelt is crucial to implement experimental set-ups that only require actions belonging to the species' natural repertoire. If we ignore interspecific differences in terms of wirkwelt, we may end up concluding that some species fall short of certain cognitive skills simply because their anatomical characteristics make the required action unnatural to the species. Adapting to the species' wirkwelt, therefore, often implies modifying our set-ups across taxa (e.g. requiring individuals to 'choose' by grabbing, approaching, touching with the nose or swimming around one of several objects), balancing the need to maintain experimental procedures both comparable across species and 'fair' to each different wirkwelt.

Consequently, the purpose of this book is to bring together leading researchers with extensive experience in the study of animal behaviour and cognition, to highlight the importance of the Umwelt concept and provide useful practical advice on how to take it into account when conducting cognitive experiments. First, researchers will introduce their study taxon, providing us with essential information on its anatomical, perceptual and socio-ecological characteristics. Then, they will explain how these characteristics may be linked to specific cognitive skills and how they may affect the choice of experimental procedures during cognitive tests. Finally, they will provide us with a series of examples and practical tips drawn by their everyday experience, to introduce the methodological tools most apt to work with their taxon.

To foster dialogue and open up to the study of novel species and methods across research areas, other scientists working with different taxa and/or methods will complement this information with small boxes within chapters. In these boxes, the authors will briefly comment (1) on the possibility to extend methods across taxa, introducing a different species with similar socio-ecological or physical characteristics, which may be tested in analogous ways ('All for one and one for all' boxes); (2) on the need to adapt methods across closely related taxa, as some socio-ecological or physical characteristics may differ deeply even across phylogenetically close taxa ('The devil is in the details' boxes); and (3) on the methodological differences and issues raised when testing wild and/or captive conspecific populations ('Wild vs. lab' boxes). This combination of chapters and boxes not only aims to help researchers to carefully plan

experiments and interpret data, but also to open up to the use of new methodologies and taxa in animal cognition.

In this book, we have included species which have attracted much attention in the study of animal cognition, and others whose cognitive skills have just started being investigated. It is therefore a first attempt to highlight the need and urge to consider each animal's Umwelt when testing cognition, and a first proposal to dive in, explore and enjoy different ways of living the same world. However, the selection of taxa is necessarily partial and arbitrary, as every single species lives in a particular Umwelt and would be worth a chapter on its own. As no taxon is more relevant or interesting than others per se, and in contrast with the idea of a *scala naturae*, we have ordered the chapters in a strict alphabetical order.

In the first chapter, Zhanna Reznikova introduces us to the extraordinary world of ANTS – eusocial insects including around 12,000 species, with highly sophisticated communication and a variety of socio-ecological characteristics. She describes original methodological approaches to study cognition in individual ants, with a special focus on social learning, problem-solving and communication. Within her chapter, Felicity Muth draws interesting theoretical and practical parallels between ants and other eusocial species, like honeybees and bumblebees (Box 1.1). Moreover, Neil Tsutsui highlights the importance of combining field and laboratory studies, providing useful suggestions on how to practically investigate cognition in wild ants (Box 1.2).

In the second chapter, Yossi Yovel and Stefan Greif introduce us to one of the most diverse groups within the mammalian order – BATS. With their immense range of foraging strategies, social behaviours and sensory systems, bats constitute an intriguing model for studying cognition. The authors provide detailed information on how to implement innovative tasks, and explain how technology can help us overcome most of the challenges related to the study of bat cognition. In their chapter, Manfred Gahr fruitfully discusses the advantages and disadvantages of different telemetric and logging devices used to work with both bats and birds (Box 2.1). Further, Rachel Page provides suggestive examples of bat species with a very different Umwelt, and warns us about the risks of ignoring these differences in comparative cognition (Box 2.2).

In the third chapter, Randolf Menzel makes us acquainted with the fascinating taxon of HONEYBEES, revealing how the study of cognition can best thrive by individually testing honeybees foraging outside their colonies. Further, he discusses how different experiments can be conducted in the lab and in the wild, with a special focus on discrimination, memory, learning and navigation. Within this chapter, Chris Faulkes explains how eusocial naked mole rats have all the characteristics (e.g. longevity, complex socio-ecological environment) to probably bear comparison with other eusocial species in terms of cognition (Box 3.1).

In the fourth chapter, Simon Ducatez, Sarah Overington, Jean-Nicolas Audet, Marine Battesti and Louis Lefebvre discuss why CARIB GRACKLES, a blackbird species successfully adapted to a highly anthropogenic environment, are a valuable model to study cognition. Moreover, they extensively explain how to test wild individuals in controlled experimental set-ups, with a special focus on innovation, personality and interindividual variation in cognition. In this chapter, Noam Miller describes a further

approach to investigate bird cognition – the study of collective movement and decision-making, which has been successfully used across a variety of taxa (Box 4.1). Finally, Lucy Aplin discusses the importance of testing cognition in even more natural set-ups and provides a series of elegant examples on how to do that (Box 4.2).

In the fifth chapter, Cinzia Chiandetti and Giorgio Vallortigara introduce us to the Umwelt of CHICKEN – a domestic species which has proven an excellent model for the study of early learning, memory consolidation and core knowledge, including understanding of numbers, space and objects. The authors describe a series of methodological approaches that can be used to successfully test cognition in chicks and discuss how they can crucially complement studies carried out with mammalian models. Within their chapter, Luigi Baciadonna and Alan McElligott draw unexpected parallels between cognition in chicks and goats, focusing on the role played by domestication on the evolution of cognitive skills (Box 5.1). In her Box 5.2, Carolynn K-lynn Smith familiarizes us with the wild counterpart of chicken, red jungle fowls, and stresses the socio-ecological and cognitive differences between the two subspecies.

In the sixth chapter, Roman Wittig and Catherine Crockford make us acquainted with our closest living relatives – CHIMPANZEES. Starting from chimpanzees' complex ecological and social system, they guide us through the amazing behaviour of this species in the wild and back to the evolutionary roots of human cognition. By focusing on this species' spatial skills, tool use and social cognition, the authors introduce readers to different possible experimental set-ups, including play-back experiments and object presentations. Within this chapter, Christian Rutz explains how a phylogenetically distant taxon, corvids, underwent convergent evolution, and how methods can be creatively extended from chimpanzees to corvids, and vice versa (Box 6.1). Finally, Julia Fischer convincingly discusses the importance of fostering dialogue between lab- and wild-based studies of primate cognition, trying to bring together both approaches (Box 6.2).

In the seventh chapter, Volker Deecke brings us over the ocean to observe DOLPHINS AND WHALES in their natural environment. While describing the variety of socio-ecological characteristics of these mammals, their sensory systems and cognitively skills uniquely adapted to the underwater world, he provides practical solutions to the multiple challenges of studying cognition in the wild, with a special focus on social behaviour, foraging and navigation. Moreover, Filippo Aureli and Colleen Schaffner draw our attention to one crucial aspect of social complexity, and remind us of the possible cognitive challenges faced by taxa characterized by high levels of fission–fusion (Box 7.1). In Box 7.2, Frants Havmand Jensen describes the peculiar Umwelt of deep-water whales, which likely posits special cognitive challenges not only to these cetaceans, but also to the researchers aiming to test them.

In the eighth chapter, Lucy Bates introduces us to one of the most long-living, large-brained and socially complex taxa we know – ELEPHANTS. She provides us with practical recommendations on how to implement socio-ecologically relevant cognitive studies in the wild and suggests possible future directions for cognitive research, in line with the elephants' Umwelt. Within this chapter, Phyllis Lee draws further attention to elephants' social cognition and complex social strategies, drawing interesting parallels with other taxa (Box 8.1).

In the ninth chapter, Catarina Vila Pouca and Culum Brown successfully condense our current knowledge on perception, socio-ecology and cognition in the group of vertebrates with the largest radiation – FISH. Although fish possess many anatomical and perceptual adaptations to the aquatic environment, the authors describe how most experimental procedures used to study cognition in other species (including spatial and social learning) are readily adaptable to fish. In this line, Jonathon Crystal takes things further and discusses different approaches to study memory across taxa, including fish (Box 9.1). Finally, Michael and Barbara Taborsky highlight the peculiarities of Cichlids, a group of fish with very unusual perceptual, social and cognitive characteristics (Box 9.2).

In the tenth chapter, Robert Elwood brings us inside the fascinating world of HERMIT CRABS, whose cognitive skills are still at an incipient stage of research. He describes a series of studies on shell investigation and shell preferences, to provide us with a socio-ecologically relevant approach to the study of cognition in this taxon, with a special focus on decision-making and planning. In Box 10.1, Erin McCallum and Sigal Balshine draw interesting parallels between hermit crabs and a small territorial fish, the round goby, which also competes for access to shelters. Finally, Mark Laidre discusses important differences across hermit crab species and meets the challenge of proposing possible experimental approaches to study hermit crabs in the wild (Box 10.2).

In the eleventh chapter, Lily Johnson-Ulrich, Kenna Lehman, Julie Turner and Kay Holekamp bring us to sub-Saharan Africa to study spotted HYENAS – scavengers with extended juvenile periods and complex societies. Especially focusing on their social cognitive skills and innovation abilities, they effectively explain how to conduct controlled experiments in wild and captive settings, using a variety of methodological approaches. In her Box 11.1, Friederike Range complements this information by discussing similarities and differences between hyenas, dogs and wolves, both in terms of cognition and experimental approaches required.

In the twelfth chapter, Martin Whiting and Daniel Noble introduce us to the mesmerizing Umwelt of LIZARDS, especially focusing on inter- and intraspecific differences in cognition. By providing us with useful practical examples, they explain how to test their cognition, including social learning and behavioural flexibility, according to the lizards' Umwelt. In his Box 12.1, Michael S. Grace further discusses the challenges of testing cognition in reptiles, with a series of suggestive examples from the study of snake cognition. Finally, David Steinberg and Manuel Leal explain why the unique Umwelt of lizards may posit special constraints when testing them in captive settings and propose possible approaches to the study of wild populations (Box 12.2).

In the thirteenth chapter, Marta Manser makes us acquainted with a cooperative breeding mongoose species – MEERKATS. She extensively discusses examples of successful research approaches to study the cognitive mechanisms involved in their complex social systems, elaborate vocal and olfactory communication and social learning, with a further focus on the pervasive effect of hormones on their social behaviour. Judith Burkart starts from the meerkats' cooperative breeding system to discuss the cognitive challenges they may face, and the possibility to successfully

extend methodological approaches across different cooperative breeders (Box 13.1). Finally, Alex Thornton draws interesting parallels between meerkats and other closely related mongoose species, providing unique research opportunities to understand the selective pressures driving cognitive evolution (Box 13.2).

In the fourteenth chapter, Jennifer Mather and Michael Kuba bring us deep into the water to observe cognitive skills in OCTOPUSES. They explain how to investigate their personalities, play behaviour and learning skills, taking into account the striking peculiarities of their neural and behavioural systems. Within their chapter, Chuan-Chin Chiao discusses how, despite socio-ecological differences and phylogenetic distance, squids and cuttlefish share with octopuses similar body patterns for camouflage and communication, fostering interspecific comparisons by creative researchers in animal cognition (Box 14.1).

In the fifteenth chapter, Irene Pepperberg highlights the peculiar Umwelt characterizing her study species – grey PARROTS. She especially focuses on their vocal skills, which have proved a valuable way to implement unique methodological approaches to the study of cognition and language in this taxon. In Box 15.1, Stephanie King discusses some striking similarities between cognition (including vocal labelling) in parrots and bottlenose dolphins, and the similar methodological approaches that can be used in both taxa.

In the sixteenth chapter, Tristan Guttridge, Kara Yopak and Vera Schluessel describe SHARKS – a group of cartilaginous fishes with an incredible range of anatomical, foraging and social characteristics. The authors describe how technological advances (including biotelemetry and bio-logging techniques) have allowed researchers to broaden experimental investigations of cognition in these species. In Box 16.1, Stewart Nicol draws an unexpected parallel between sharks, which are 'atypical fishes', and monotremes, which are 'atypical mammals', providing inspiring inputs to test cognition in the latter. Finally, David Jacoby proposes interesting methodological approaches to study cognition in wild sharks and rays (Box 16.2).

In the seventeenth chapter, Elizabeth Jakob, Skye Long and Margaret Bruce discuss how the peculiar perceptual system of jumping SPIDERS makes them an ideal taxon to test cognition. The authors explain how their Umwelt posits specific challenges to researchers, and how these challenges can be easily met by carefully planning experiments. Within this chapter, Cole Gilbert highlights significant differences and similarities with tiger beetles and other species (Box 17.1). Furthermore, Fiona Cross provides convincing evidence that different species of spiders, even if belonging to the same family, may call for essential changes in experimental procedures (Box 17.2).

Finally, in the eighteenth chapter, Anna Wilkinson and Ewen Glass guide us through the amazing world of cold-blooded cognition to discover TORTOISES – a taxon which has long been ignored in the study of animal cognition. They provide useful tricks and original methodological approaches to successfully study visual and spatial cognition, social learning and memory. In his Box 18.1, Gordon Burghardt draws fascinating comparisons among tortoises and other reptiles, and draws attention to potential terminological caveats. Finally, Timothy C. Roth II and Aaron Krochmal stress the importance of testing tortoises in the wild, thoroughly discussing the advantages of such an approach (Box 18.2).

In its form, this book is therefore the result of a huge cooperation among experienced researchers, who have agreed to 'open the doors' of their laboratories and field sites, and to share with us their extensive first-hand knowledge about their study species. Through this book, we hope that readers will not only be fostered to reflect on the key role played by the Umwelt in animal cognition, but also stimulated to consider possible ways to work with novel species and methods.

The study of animal cognition is thrilling and provides creative minds with endless opportunities to come up with relevant research questions and novel methods to address them. We hope that this book will be successful in further fostering this development, facilitating interdisciplinary dialogue and inspiring new and old scholars to enthusiastically approach the study of different taxa, embrace new methodological approaches and generously share their knowledge. The immense diversity of different worlds inside the same world is our richness: to admire, protect and investigate.

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