Convergent cognitive evolution: what can be learnt from comparisons with corvids and cephalopods?

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Preface

This thesis is the result of my own work and includes nothing which is the outcome of work done in collaboration except as stated in the Declaration and specified in the text.

This thesis is not substantially the same as any work that I have submitted before, or, is being concurrently submitted for any degree or other qualification at the University of Cambridge or any other University or similar institution except as declared in the Preface and specified in the text.

I further state that no substantial part of my thesis has already been submitted, or, is being concurrently submitted for any such degree, diploma or other qualification at the University of Cambridge or any other University or similar institution except as declared in the Preface and specified in the text.

This thesis does not exceed the prescribed word limit for the relevant Degree Committee.

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Thesis title

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Summary

Emery and Clayton (2004) proposed that corvids (e.g. crows, ravens, jays) may have evolved – convergently with apes – flexible and domain general cognitive tool-kits. In a similar vein, others have suggested that coleoid cephalopods (octopus, cuttlefish, squid) may have developed complex cognition convergently with large-brained vertebrates but current evidence is not sufficient to fully evaluate these propositions. The aim of my thesis is to gain further insight into these issues.

My first objective is to further our understanding of how deep the cognitive convergence between corvids and apes may be. To this end I report four empirical studies exploring cognitive complexity among different domains in a single species of corvids, the Eurasian jay (*Garrulus glandarius*). In Chapter 2, I investigate physical problem solving, finding that jays cannot spontaneously select functional tools according to their physical properties (i.e. size, shape) but can use novel tools – sticks – to solve a familiar task. In Chapter 3, I test whether future oriented caching in jays is underpinned by future planning abilities or by spontaneous predispositions; data do not support either hypotheses. In Chapters 4 and 5, I focus on social cognition. I find no indication that jays can integrate the visual perspective and current desire of competitors to protect their caches. Surprisingly, jays could also not respond to either of the two social cues independently, thus questioning the reliability of previously reported caching strategies.

My second objective is to lay theoretical and methodological groundwork for studying convergent cognitive evolution between cephalopods and large-brained vertebrates. Therefore, in Chapter 6 I propose an evolutionary hypothesis for the emergence of large brains and behavioural flexibility in cephalopods and put forward novel paradigms that may allow researchers to explore the cognitive underpinning of octopus' complex behaviours.

I conclude by discussing the implication of my findings and future directions for the study of convergent cognitive evolution in corvids and cephalopods.

Declaration

The work in this thesis was carried out under the supervision of Professor Nicola S. Clayton and Doctor Ljerka Ostojić at the Department of Psychology and in Clayton's Comparative Cognition Laboratory at the Sub-Department of Animal Behaviour at the University of Cambridge where the corvids were housed.

In Chapter 2, the experiments were designed in collaboration with Sarah Jelbert. Markus Boeckle was involved in the analysis and interpretation of data. Ben Farrar acted as second observer for the inter-observer reliability.

In Chapter 3, the experiments were designed by Johanni Brea (EPFL, Switzerland) and Ljerka Ostojić. In Experiment 3.1, Ben Farrar and Ljerka Ostojić were involved in data collection. The statistical analysis of the data of Experiment 3.1 and 3.2 (Appendix C) was conducted in collaboration with Johanni Brea.

In Chapter 4, the experiments were designed by Christopher Krupenye (University of St. Andrews) and Ljerka Ostojić. In Experiment 4.1, Ben Farrar and Ljerka Ostojić were involved in data collection.

In Chapter 5, the experiments were designed in collaboration with Ljerka Ostojić.

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Contents

Publications

Chapter 2 includes content from:

Amodio P., Boeckle M., Jelbert S. A., Ostoijć, L., & Clayton N. S. (**Accepted** in *Animal Behavior and Cognition*). How flexible is tool use in Eurasian jays (*Garrulus glandarius*)?

Chapter 3 includes content from:

Amodio* **P.**, Brea* J., Farrar B., Ostojić L., & Clayton N. S. (**In prep.**). Testing two competing hypotheses for Eurasian jays caching for the future: planning versus compensatory caching.

Chapter 4 includes content from:

Amodio P., Farrar B., Krupenye C., Ostojić L., & Clayton N. S. (**In prep.**). Can Eurasian jays (*Garrulus glandarius*) integrate others' desires and perspectives to protect their caches?

Chapters 6 and 7 include content from:

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Publications not included in this thesis:

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Amodio P. (2019). Octopus intelligence: The importance of being agnostic. *Animal Sentience,* 26(20).

Amodio P., Boeckle M., Schnell A. K., Ostojić L., Fiorito G., & Clayton N. S. (2019). Shell Loss in Cephalopods: Trigger for, or By-Product of, the Evolution of Intelligence? A Reply to Mollo et al. *Trends in Ecology and Evolution,* 34, 690–692. doi:10.1016/j.tree.2019.05.005.

Amodio P., Jelbert S. & Clayton N. S. (2018). The interplay between psychological predisposition and skill learning in the evolution of tool use. *Current Opinion in Behavioral Sciences,* 20: 130-137. doi.org/10.1016/j.cobeha.2018.01.002.

Schnell A. K., **Amodio P.**, Boeckle M., & Clayton N. S. (**Under review** in *Biological Reviews*). Comparing the convergent minds of cephalopods and corvids: an applied review.

Amodio P., Shigeno S., & Ostojić L. (**In prep.**, invited contribution to *Essential for Life Science, eLS*). Evolution of intelligence in Cephalopods

CHAPTER 1:

Introduction

All animals must attain the same basic goals: acquire food, find shelters, avoid predators and sire offspring. Yet the complexity of the cognitive adaptations to fulfil these shared needs differ dramatically among species. Some groups of animals evolved flexible cognitive machineries to meet the challenges of surviving and reproducing, whereas other groups developed simple sets of hardwired predispositions for the same purpose. Understanding the processes leading to the emergence of cognitive sophistication is one of the most fascinating issues in evolutionary biology and comparative cognition. This is particularly the case when considering that intelligence is one of the characterizing features of our species.

In this introductory chapter I will first present the main hypotheses for the evolution of intelligence, and review the evidence suggesting that complex cognition may have evolved multiple times independently in distantly related taxa. I will then turn my attention to two groups of large-brained animals, the corvids (birds in the crow family, which includes the jays, magpies and ravens) and the coleoid cephalopods (octopus, cuttlefish and squid), and outline unanswered key questions in regard to the evolution of their cognition. However, before doing so, it is essential to provide some background of what it is meant by 'Intelligence'.

1.1: WHAT IS INTELLIGENCE?

> 'Using the term animal intelligence is a calculated gamble. It has the substantial advantages of communicating the general topic of interest to a wide audience in many different fields and of emphasizing the broad range of phenomena to be included. But it also carries a substantial disadvantage. […] When technical discussion begins, then, there is a risk of misunderstanding based on people's assuming different definitions of animal intelligence.' (Kamil, 1994, page 21).

'Intelligence' is a contentious word, lacking a univocal definition (Legg and Hutter, 2007). At first, one may be prone to think that the ambiguity of the term results from its wide applicability: humans, animals, as well as robots can be referred to as intelligent agents, both among scientists and non-specialists. Yet, no consensus exists even within specific research areas, nor when intelligence is used to describe only a specific class of agents. This is particularly true in the case of non-human animals, whose cognitive capacities vary dramatically among species, and who are the subject of investigation by a number of scientific fields (e.g. cognitive ecologists, comparative psychologists, evolutionary anthropologists) adopting different research approaches.

According to some authors, animal intelligence can be defined as *the ability* of an organism to solve problems occurring in its natural and social environment (Roth, 2015; Roth and Dicke, 2005), whereas in others' view animal intelligence should be thought as *an aggregate* of specific cognitive abilities that a species may have (cf. Roth and Dicke, 2005; Shettleworth, 2010). Although far from being trivial, the issue of whether intelligence should be conceived as a single capacity or as a set of abilities is not the only, or even the most critical argument of dispute. Different fields have the propensity to frame the problem of animal intelligence from different perspectives, and sometimes to adopt a focus on distinct levels of explanation (e.g. ultimate, proximate levels; Tinbergen, 1963). For instance, an evolutionarily-driven approach may lead towards defining biological intelligence in terms of fitness or other adaptive benefits, whereas comparative psychologists tend to characterize intelligence in terms of cognitive mechanisms (Kacelnik, 2006). A typical approach in the latter field is to define intelligence by exclusion, rather than through a positive description of the mechanisms underpinning it (Seed et al., 2009a). In a nutshell, behaviours that appear complex and flexible might be considered evidence of intelligence – or complex cognition – if it can be empirically demonstrated that such behaviours are not the expression of hardwire predispositions (e.g. genetic canalization) or simple learning processes, such as associative learning (Heyes, 2012; Seed, 2007)[1]. Thus, from the comparative cognition perspective, intelligence and complex cognition are often used as synonymous. This approach can foster a dichotomous view of cognition, with the risk of dismissing crucial nuances (Call, 2010; Penn and Povinelli, 2007a). In contrast, our understanding of animal intelligence may be substantially increased by exploring how putatively independent mechanisms (e.g. associative learning, 'complex cognitive abilities') could

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[1] Henceforth I will use 'complex cognition', as well as 'enhanced cognition', to refer to those cognitive underpinnings of flexible behaviours that cannot be described in terms of simple mechanisms, i.e. hardwired predisposition and/or associative learning.

together underpin a given behavioural response (Cheke et al., 2011). Further, the rationale for privileging simple over complex cognitive processes (e.g. behaviour-reading over mind-reading) in the light of parsimony has been challenged both on theoretical and methodological grounds (e.g. Bausman and Halina, 2018; Dacey, 2016). However, a key benefit of this approach is that it provides a straightforward 'operational guidance' to investigate intelligence by observing the behaviour of non-verbal species.

1.2: HOW CAN INTELLIGENCE BE MEASURED?

Intelligence is a cognitive feature and as such it cannot be measured directly. Typically, two kinds of proxies are used to quantify this trait. On the one hand, a number of neuroanatomical measures have been proposed as indicators of cognitive complexity. Some of the most popular indicators are those measuring relative brain size, i.e. brain size corrected for body size. For instance, the encephalization quotient (EQ) is the ratio between the brain size observed in a species and the brain size that would be expected given the body size of that species, with the latter being corrected by an allometric exponent (Jerison, 1973). Because brain size scales allometrically to body size, species with high EQs are thus considered as more intelligent (Jerison, 1985; Marino, 1998; Roth and Dicke, 2005). Another popular view suggests that cognitive complexity should be quantified by considering the size of the neural substrates responsible for complex cognition (e.g. neocortex in primates, pallium in birds), either as absolute measurement or in relation to the whole brain (Byrne and Corp, 2004; Sayol et al., 2016; Shultz and Dunbar, 2010). Both relative brain size and neocortex measurements (or equivalent for non-mammals) seem to correlate positively with a number of features among birds and primates, including tool use, innovation, and social learning (Boire et al., 2002; Lefebvre et al., 1997, 2004; Reader and Laland, 2002). However, it is debated whether these measurements represent the best indicators of the cognitive capacity of a species (for a recent review see Dicke and Roth, 2016; Healy and Rowe, 2007). For instance, Deaner et al. (2007) found that absolute brain size is more informative at explaining the variability of general intelligence in primates. In sharp opposition, others have challenged the link between intelligence and brain size (Chittka and Niven, 2009; Logan et al., 2018), and argued that alternative proxies, such the total number of neurons in the brains or in specific neural areas should be used instead (Herculano-Houzel, 2011;

Olkowicz et al., 2016). Thus, to date there is no consensus on which neuroanatomical measure can more effectively formalize the relationship between brain and intelligence.

On the other hand, a complementary approach for quantifying intelligence is through behavioural proxies. Behavioural flexibility is often considered as the gold standard evidence for complex cognition in non-human animals (Roth, 2015). Different definitions have been put forward to describe behavioural flexibility (or plasticity), including 'the ability to switch readily among alternative strategies in order to solve problems' (Holekamp et al., 2013, page 2)[2], as well as 'the ability of an individual to directly respond and adjust its behaviour to environmental stimuli' (Coppens et al., 2010, page 4022). The rationale behind the use of this proxy is that flexible behaviours should be expressions of cognitive processes, thereby the higher the level of flexibility observed in a given behavioural response, the more complex is its cognitive underpinnings (Mikhalevich et al., 2017). This assumption, and the general idea that behavioural flexibility *per se* can be taken as evidence of complex cognition, has been challenged. For instance behavioural flexibility does not correlate with problem solving efficiency, nor with learning speed in great-tailed grackles (Logan, 2016). Despite the criticisms, behavioural flexibility remains to be frequently used to quantify cognitive complexity across a wide range of species, from primates to birds and from reptiles to fishes (e.g. Amici et al., 2018; Leal and Powell, 2012; Lucon-Xiccato and Bisazza, 2014; Sol et al., 2002; Wilkinson and Huber, 2012).

In sum, neither the neuroanatomical or the behavioural proxies that are currently used to quantify intelligence are exempt from concerns. Yet, in my view, these proxies are important sources of information. Thus, rather than abandoning them, we should consider them jointly and critically. A single line of evidence – e.g. a study showing that species X has a large relative brain size, or can perform flexible behavioural responses to solve a task – should be taken only as an *indication* – rather than as *demonstration* – that the species may be endowed with complex cognition. The stronger and more consistent the evidence from multiple studies in a given species or group from both neuroanatomical and behavioural measurements, the stronger the confidence that can be given to the proxies as indicators of intelligence. Thus, in this thesis, I will attempt to convey a critical evaluation of the neuroanatomical and behavioural evidence of intelligence in non-human animals when discussing their cognitive complexity.

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[2] It is Holekamp et al. (2013)'s definition of 'behavioural flexibility' that I will adopt throughout the thesis.

1.3: WHEN DOES INTELLIGENCE EVOLVE?

The question of why some species are equipped with higher cognitive sophistication than others can effectively be addressed by asking: which are the factors selecting for enhanced cognition? This issue has been traditionally investigated in primates, thus resulting in a number of hypotheses for the evolution of intelligence within this group. The most accepted hypotheses can be divided into two categories, which are often referred to with the umbrella terms of 'Ecological Intelligence Hypothesis' and 'Social Intelligence Hypothesis'. These two groups of hypotheses differ in one key respect: the kind of evolutionary pressure that is posited to have fostered the emergence of intelligence.

The Ecological Intelligence Hypothesis posits that complex cognition evolved to meet specific challenges associated with foraging activities (for a recent review see Rosati, 2017). One of these challenges may have been the need to locate ephemeral resources: species relying heavily on spatiotemporal dispersed foods (e.g. ripe tropical fruits) may face stronger pressures than those feeding on frequent and abundant foods (e.g. leaves), such that enhanced cognitive abilities may have evolved in the formers to optimize foraging activities (Milton, 1981). Specifically, sophisticated memory and spatial navigation may confer substantial benefits in terms of keeping track of depleted patches, remembering locations of fruit-bearing trees, and taking efficient routes to reach target areas. Further, a study in chimpanzees (*Pan troglodytes*) suggests that this kind of ecological problem may also have favoured the emergence of future planning abilities (Janmaat et al., 2014; but see Thom and Clayton, 2015). Supporting the role played by spatiotemporal dispersed food in the evolution of intelligence, frugivores appear to have larger brains than folivores among primates (Barton, 1996; Clutton-Brock and Harvey, 1980).

Another popular idea within the framework of the Ecological Intelligence Hypothesis suggests that extractive foraging may have acted as a key driver for the emergence of cognitive sophistication. According to Parker and Gibson (1977), the co-occurrence of generalist diets and reliance of food not directly accessible may have posed severe cognitive pressures to find hidden foods and flexibly employ sophisticated sensorimotor coordination to process a variety of embedded foods. In line with this hypothesis, manipulation complexity and brain size are positively correlated in primates (Heldstab et al., 2016). From a slightly different perspective, Byrne (1997, 2004) proposed that critical challenges may have been exerted by those forms of extractive foraging that involve the use of tools. In line with this possibility, the complexity of tool use repertoires positively correlates with the neocortex size in primates (Reader and Laland, 2002); with large-brained species such as chimpanzees, orang-utans and capuchin monkeys exhibiting particularly sophisticated behaviours: they employ a variety of objects as tools, use multiple tools in sequence to achieve a specific goal, and even manufacture composite tools (Mannu and Ottoni, 2009; Meulman and van Schaik, 2013; Moura and Lee, 2004; Sanz and Morgan, 2007, 2009; Sugiyama, 1997; Torralvo et al., 2017).

Although the capability of using tools[3] does not require complex cognition *per se* (Emery, 2013; Shumaker et al., 2011; Teschke et al., 2011, 2013), most cases of tool-mediated extractive foraging in primates are best understood as behavioural innovations (van Schaik et al., 2003; Whiten et al., 1999) rather than as the expression of genetic predispositions. Thus, it is likely that cognitive flexibility underpinning such behavioural inventions may have arisen to exploit embedded resources that otherwise would have been inaccessible. Interestingly, because embedded foods are typically highly energetic (e.g. seeds, honey, insects), the capability of exploiting such resources – either with or without using tools – may have not only posed cognitive challenges but also provided payoffs to meet the increased metabolic costs required to evolve enlarged brains (Navarrete et al., 2016).

In sharp contrast, the Social Intelligence Hypothesis accredits the evolution of intelligence to the demands of group living (for recent reviews see Byrne, 2018; Whiten, 2018; Whiten and van de Waal, 2017). Pioneeringly sketched by Jolly (1966) and evaluated more thoroughly by Humphrey (1976), the idea that primates' cognitive sophistication emerged in response to social challenges was later on formalized as the Machiavellian Intelligence Hypothesis by Byrne and Whiten (1988) and over time became the most popular explanation for the origin of intelligence. In short, the hypothesis suggests that intelligence may have evolved as an adaptation to solve the problems of complex social environments, namely to compete and cooperate with conspecifics to maximize individual payoffs. Primate groups are intricate societies, in which individuals form alliances, hunt cooperatively, reconcile after aggressive episodes,

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[3] In this thesis I refer to 'tool use' as "the external employment of an unattached or manipulable attached environmental object to alter … another object … when the user holds and directly manipulates the tool during or prior to use …" (Shumaker et al. 2011, page 5).

flexibly exchange services and goods (e.g. grooming, food), and deceive competitors (Aureli, 1992; Aureli et al., 2002; Boesch, 1994, 2002; Cheney, 1977; Hammerstein and Noë, 2016; le Roux et al., 2013). Thus, it appears plausible that enhanced cognitive capacities perhaps in terms of individual recognition, identification of others' associated (e.g. allies, relatives, partners), transitive inference of social ranks, and predicting others' behaviours may have conferred substantial benefits (Cheney et al., 1986; Seyfarth and Cheney, 2015). Crucially such cognitive challenges are not thought to be a mandatory requirement of group living, rather they are postulated to result from maintaining intense and enduring social bonds, typically with multiple members of a group (Shultz and Dunbar, 2007). Early support for this hypothesis was provided by Dunbar's work showing that neocortex size and average group size positively correlate in primates, a finding suggesting that species living in larger groups are endowed with higher cognitive power (Dunbar, 1992). Using less crude proxies for social complexity, further studies have found links between neocortex size and rate of 'tactical deception' (Byrne and Corp, 2004), frequency of coalition (Dunbar and Shultz, 2007), and size of grooming cliques (Kudo and Dunbar, 2001).

More recently, the framework of the Social Intelligence Hypothesis was enriched by the idea that social learning may have played a key role in the evolution of intelligence. Cultural traditions – behavioural innovations that spread within social units through social learning – have been identified in several species, most notably, chimpanzees, orangutans (*Pongo pygmaeus*), and capuchin monkeys (*Cebus capucinus*) (Moura and Lee, 2004; Schaik, 2003; Whiten et al., 1999), thus suggesting that social learning is a crucial aspect of primate societies. Further, frequencies of innovation and social learning correlate with proxies of brain complexity across primates (Reader and Laland, 2002). Building on this evidence, it has been argued that being exposed to cultural societies could shape and enhance the cognitive underpinnings of individuals on ontogenetic timescale and ultimately select for increased intelligence (e.g. capability to learning and innovation) at the level of species on a long-term evolutionary scale (van Schaik and Burkart, 2011; Whiten and van Schaik, 2007).

The Social Intelligence Hypothesis and Ecological Intelligence Hypothesis have been classically conceived as opposing propositions, with novel evidence supporting one of the two being used as arguments fuelling a fierce scientific debate. Yet, these hypotheses are not mutually exclusive *per se*, such that more recent approaches have worked towards frameworks accounting for both ecological and social pressures (e.g. Dunbar and Shultz, 2017; Navarrete et al., 2016).

A third relevant hypothesis proposes that intelligence might have arisen as a cognitive adaptation to cope with the challenges of predator–prey interactions (Zuberbühler and Byrne, 2006; Zuberbühler and Jenny, 2002). Capturing prey and avoiding predation have dramatic fitness consequences. Thus, it is not hard to imagine how complex cognition allowing flexible behaviours in these domains could be subject to strong positive selection. According to some authors, the cognitive challenges of predator–prey dynamics can be equivalent to those required to compete with group members as in both cases they require interactions with another individual pursuing personal gains (Byrne and Bates, 2007). Indeed, one of the most complex cases of representational communication evolved in monkeys to inform conspecifics about the kind of predator (e.g. eagle, leopard) threatening the group, and thus to allow predator-specific escape strategies (Zuberbühler, 2000a, 2000b; Zuberbuhler et al., 1997). However, this hypothesis still needs to be properly evaluated among primates.

A final consideration in regard to the conditions favouring the evolution of intelligence concerns life history. Robust evidence indicates that brain size correlates with life history among mammals (Gonzales-Lagos et al., 2010) and primates (Street et al., 2017): species with larger brains have typically slower life history trajectories (e.g. slow development, extended period of juvenility, long life span). Two different explanations have been proposed to account for this association. According to one view, slow life history emerges as a consequence of the development of enlarged brains, due to the fitness advantages conferred by increased cognitive capacities (e.g. reduced extrinsic mortality; Allman et al., 1993; Sol, 2009a, 2009b, but see Liedtke and Fromhage, 2019). In contrast, the alternative explanation proposes that slow life histories are a by-product of brain growth: enlarged brains imposed longer pre- and post-natal developmental periods, such that slower life histories trajectories may be an unavoidable by-product (Barton and Capellini, 2011).

In sum, evidence indicates that intelligence may have evolved in primates in response to socio-ecological pressures and in association with slow life history.

1.4: CONVERGENT COGNITIVE EVOLUTION

How do similar adaptations evolve in different groups?

Different evolutionary processes can lead to the emergence of similar traits in more than one lineage. Similar traits can either be inherited from a common ancestor (homologous adaptations) or evolve multiple times independently (analogous adaptations) in response to comparable evolutionary pressures. The principle of parsimony is invoked to distinguish between these two possibilities, such that similar traits exhibited by different species/groups tend to be considered as homologous if the minimum number of independent events required for this evolutionary process to occur is smaller than that necessary for the evolution of analogous traits (Richter, 2005). For instance, tunas (*Scombridae* family), dolphins (*Delphinoidea* family) and lamnid sharks (e.g. great white shark, *Lamnidae* family) share a variety of morphological adaptations (e.g. high streamlines body shape, lunate caudal fin, etc.) that allow fast swimming, thus supporting a lifestyle of open-water predators (Donley et al., 2004; Pabst, 2000). When these traits are investigated within each of the two families (e.g. in yellowfin tunas and bluefin tunas), such adaptations are likely to represent homologous traits that evolved once in the common ancestor and were subsequently inherited by extant species. This is because the alternate explanation is less parsimonious: e.g. yellowfin tunas and bluefin tunas descended from a common ancestor who lacked such adaptations, and they developed them twice, independently. In contrast, when the evolution of these traits in dolphins, tunas and lamnid sharks is considered, then the very same traits are best understood as analogous adaptations that evolved independently in each family to support a similar lifestyle (Donley et al., 2004; Pabst, 2000). It is quite unlikely that this specific hydrodynamic morphology evolved once in the common ancestor of fish and cetaceans, and subsequently disappeared repeatedly in others groups of vertebrates but was retained among tunas, some sharks and dolphins.

A further distinction can be made in regard to the evolution of analogous traits. Such adaptations are considered as the outcomes of either parallel or convergent evolution, depending on whether multiple lineages evolved the trait from *similar* or *different* underlying mechanisms (i.e. genetic and developmental pathways) respectively (Arendt and Reznick, 2008; Haldane, 1932; Simpson, 1952). Most often – particularly in the lack of detailed knowledge of the genetic and developmental pathways underlying an adaptation – the taxonomic distance between the groups sharing a similar trait is used to distinguish between the two processes. Specifically, it is thought that the greater the distance between the groups, the higher the chance that the analogous trait is the result of convergent (rather than parallel) evolution. However, cases in which closely related species develop analogous traits through different underlying mechanisms have been found (e.g. Hoekstra et al., 2006), such that this assumption should be treated with caution. Further, because phenotypes are often the expression of several interacting mechanisms, clear-cut distinctions between parallel and convergent evolution can be illusory; these processes may be better viewed as a continuum than as a dichotomy (Arendt and Reznick, 2008; but see Leander, 2008). For instance, the evolution of camera-type eyes in vertebrates and cephalopods is a recurrent textbook example of convergence (Serb and Eernisse, 2008). Yet, genetic similarities between the cephalopods and vertebrates have been found, such that according to some authors camera-type eyes emerged in these groups through parallel evolution (Tomarev et al., 1997).

Despite their differences, both parallel and convergent evolution are processes triggering the development of independent solutions by different species/groups to solve similar problems. As such, the study of these processes is central to understand the conditions selecting a specific adaptation. By focusing on more than one lineage which independently evolved an adaptation, it is possible to overcome the idiosyncrasies of a given group (e.g. evolutionary history, habitat), and thus to gain insight into the fundamental features of the process (e.g. key selective pressures; Van Horik et al., 2012). This research approach is not constrained to the study of genetic or morphological traits, rather it can be equally applied to behavioural and cognitive adaptations (e.g. MacLean et al., 2012), and thus to intelligence.

How many times did intelligence evolve?

Primates, and great apes in particular, have been traditionally considered as the pinnacle of cognitive complexity. Yet in the last few decades, indicators of complex cognition (i.e. large brains, behavioural flexibility) have been reported in a number of distantly related lineages, most notably, cetaceans, elephants, corvids and parrots (e.g. Auersperg et al., 2011; Foerder et al., 2011; Krützen et al., 2005; Raby et al., 2007; von Bayern et al., 2018). This evidence raises the possibility that similar levels of cognitive sophistication are shared among primates and other groups. If this is the case, then which evolutionary process may have produced this outcome? These groups differ dramatically in their evolutionary histories and brain features, such that it is unlikely that they may have inherited intelligence from a common ancestor. In contrast, it seems far more plausible that intelligence represents an analogous adaptation which emerged multiple times independently (Roth, 2015), through the evolution of distinct neural substrates supporting equivalent cognitive sophistication (e.g. avian nidopallium and mammalian cortex; Clayton and Emery, 2015; Güntürkün and Bugnyar, 2016; Fig. 1.1). Despite these differences, the socioecological challenges faced by cetaceans, elephants, corvids, and parrots appear to be comparable to those of apes. Most species of these lineages have complex foraging niches (e.g. omnivorous diets, reliance on spatiotemporally dispersed food, extractive foraging) and engage in long-lasting social bonds involving intense cooperation, competition and learning from conspecifics (Byrne et al., 2009; Clayton and Emery, 2007; Connor, 2007; Emery, 2006; Grodzinski and Clayton, 2010). Furthermore, as with primates, a tight link between brain size and slow life history also exists in birds and other mammals (Gonzales-Lagos et al., 2010; Minias and Podlaszczuk, 2017; Wirthlin et al., 2018). Thus, taken together this evidence led researchers to hypothesize that intelligence might have evolved convergently (or parallelly, Osvath et al., 2014) in these groups in response to similar selective pressures and through similar life history trajectories (Emery and Clayton, 2004; Fox et al., 2017; Marino, 2002; Plotnik and Clayton, 2015; Seed et al., 2009a).

In addition to these groups of large-brained vertebrates, there are two groups of invertebrates in which remarkable indications of cognitive complexity have also been reported, namely the coleoid cephalopods (cuttlefish, squid, and octopuses (Hanlon and Messenger, 2018) and the hymenoptera (e.g. bees, wasps; Chittka, 2017; Loukola et al., 2017; Perry et al., 2017; Solvi et al., 2020). Coleoids cephalopods in particular are typically considered to be the most cognitively advanced group of invertebrates: these shell-less molluscs are endowed with a sophisticated nervous system (Fig. 1.1), which resembles that of vertebrates in both relative size (Packard, 1972) and complexity (Hochner et al., 2006; Young, 1991), and exhibit high behavioural flexibility in different contexts, including predatory avoidance (Norman et al., 2001; Staudinger et al., 2013a), foraging (Forsythe and Hanlon, 1997; Mather, 1991a) and mating (Brown et al., 2012; Huffard et al., 2010). Some authors have suggested that cephalopods may have, convergently with apes and corvids, evolved a flexible and domain-general cognitive tool kit (Mather and Dickel, 2017). However, these claims should be treated with great caution given that the cognitive underpinnings of cephalopods' behavioural flexibility are still largely unexplored and because a careful evaluation of the main hypotheses for the evolution of intelligence has not yet been conducted for this group.

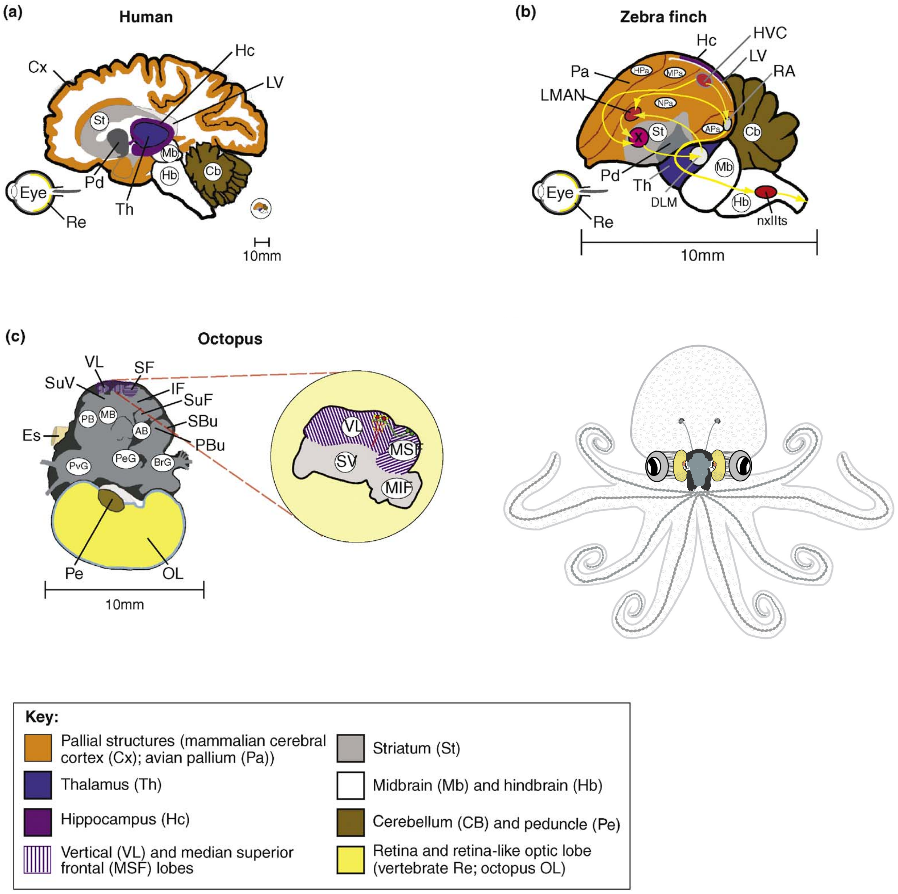

Figure 1.1: Comparison among the mammalian, avian and cephalopod brain. (a) Midline sagittal section of a human brain showing major structures. (b) Midline sagittal section of the brain of a zebra finch, a songbird. Major neural structures are shown, including those with mammalian homologs. (c) Midline section of the brain of an octopus (*O. vulgaris*). Most major lobes and ganglia are shown. Vertical (VL) and medial superior frontal (MSF) lobes (purple hatched lines), containing circuitry critical for long-term memory, are shown in a magnified view in a circular inset on the right. The key (bottom of figure) shows color-coding of major brain regions to indicate homology or functional and/or structural analogy. Other regions of human and avian brains are labelled: LV, lateral ventricle; Pd, pallidum. Pallial divisions of the avian cerebrum are indicated as follows: HPa, hyperpallium; MPa, mesopallium; NPa, nidopallium. Components of the avian anterior forebrain pathway are indicated as follows: DLM, medial nucleus of the dorsolateral thalamus; HVC, higher vocal centre; LMAN, lateral magnocellular nucleus of the anterior neostriatum; nxIIts, tracheosyringeal portion of the hypoglossal nucleus; RA, robust nucleus of the archistriatum. Major lobes and ganglia of the octopus brain are indicated as follows: AB, anterior basal lobe; BrG, brachial ganglia; Es, esophagus; IF, inferior frontal lobe; MB, median basal lobe; MIF, medial inferior frontal lobe; PBu, posterior buccal lobe; Pe, peduncle; PeG, pedal ganglia; PB, posterior basal lobe; PvG, palliovisceral ganglia; SuV, subvertical lobe; SBu, superior buccal lobe; SF, superior frontal lobe; SuF, subfrontal lobe. (Adapted from Edelman and Seth, 2009, and Shigeno et al., 2018).

The caveat of convergence: the level of analysis

For explanatory purposes, I have so far disregarded a key requirement in the study of convergence evolution, namely the identification of the level of analysis. Convergent adaptations are similar, yet not identical traits, such that the analysis of analogous adaptations in different groups will inevitably highlight differences, as well as similarities. For instance, the independent emergence of wings in birds and baths is a textbook example of convergent evolution. At a superficial level of analysis, wings in the two groups are functionally and structurally similar, i.e. these structures derived from modified ancestral forelimbs to allow flight through flapping movements. Yet at a deeper level of analysis, the structure of wings differs between the groups: birds developed wings through the elongation of forelimb bones, whereas bats acquired wings through the extension of digits bones (Seed et al., 2009a). Hence, when a process of convergent evolution is proposed it is crucial to specify the level of analysis at which two independently evolved traits may have become similar (Doolittle, 1994; Marr, 1982). Addressing this issue is not a straightforward task when the trait being investigated is intelligence, a cognitive adaption which lacks of a universally accepted definition and that can only be measured indirectly. With this in mind, when it is said that two lineages share comparable cognitive sophistication (or intelligence) as result of a process of convergent cognitive evolution, what it is actually meant to be similar? According to Seed (2007), three levels of analysis can be applied to the investigation of convergent cognitive evolution[4]. At a first and more superficial level, two distantly related groups may converge behaviourally, namely they can exhibit behaviours that appear comparably complex and flexible. At a second level of analysis, a deeper kind of convergence may occur when such flexible behaviours result from the evolution of complex cognitive underpinnings (i.e. behaviours that are not the expression of hardwired predisposition or simple learning processes) in both groups. Finally, at the third and finer-grained level, convergent cognitive evolution involves the independent emergence of similar cognitive mechanisms underlying complex behaviours in different groups. By allowing an explicit identification of the level of analysis and by providing a stepwise framework for

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[4] Note that alternative frameworks have been proposed to investigate convergent evolution. For instance, building on Marr (1982)'s work, Seed et al. (2009a) suggest that the study of cognitive convergence should be based on the following levels of analysis: computation, representation and algorithm, and implementation. In the present thesis, I adopt Seed (2007)' framework because it conveys, in my view, the most straightforward classification of the levels of analysis for investigating cognitive convergence.

studying analogous cognitive adaptations, this approach represents a useful tool to investigate convergent cognitive evolution.

Corvids and cephalopods as model groups for studying the evolution of intelligence

Among the groups of animals in which indicators of intelligence have been reported, corvids and coleoid cephalopods (henceforth cephalopods) are perhaps the most intriguing cases. These groups exhibit the most dramatic difference in brain features and evolutionary history with primates (Figs. 1.1, 1.2). The *Corvidae* are a family of oscine passerine birds that contains more than 100 species, including crows, jays, and magpies (Goodwin, 1986). The avian brain has a nuclear structure, whereas the mammalian brain is laminar (Clayton and Emery, 2015; Jarvis et al., 2005). These two alternative neural organizations resulted from approximately 300 MYA of independent evolution (Osvath et al., 2014). On the other hand, coleoid cephalopods are a successful group of shell-less molluscs encompassing more than 800 species among octopuses, cuttlefish and squid (Jerep et al., 2014). These molluscs diverged from vertebrates approximately 550 MYA ago. Cephalopods' brain is formed by the aggregation of several enlarged ganglia that show the typical neuronal arrangement of invertebrates, with cell bodies surrounding internal layers of synaptic connections (Young, 1971).

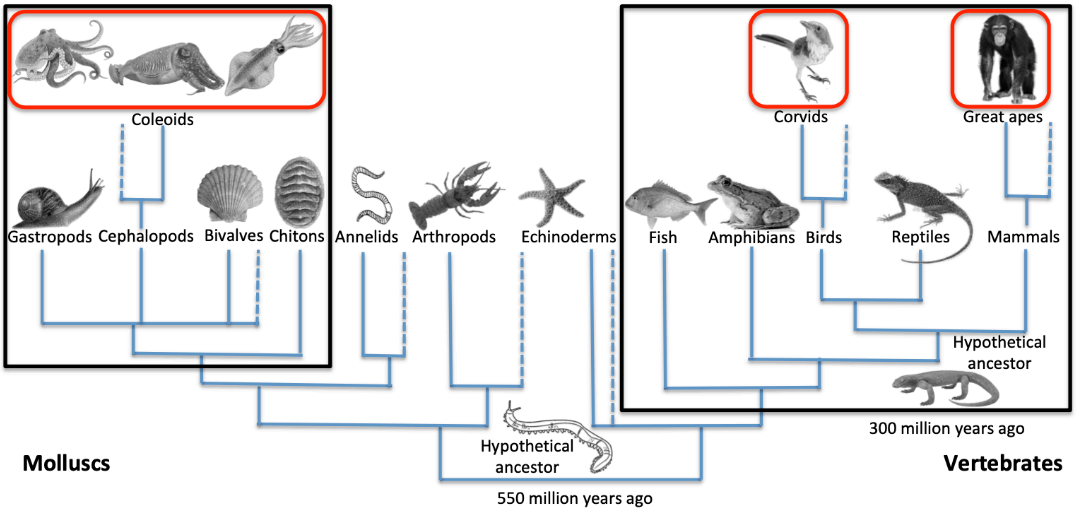

Figure 1.2: Phylogenetic tree depicting the evolutionary relationship between corvids, cephalopods and great apes. (Credit: Alexandra K. Schnell)

Corvids and cephalopods are particularly interesting models also from another perspective. While most other groups of large-brained animals encompass a small number of species (e.g. apes, elephants) and/or inhabit only specific geographic ranges, such as the tropics (e.g. parrots), corvids and cephalopods are both highly specious lineages, characterized by an enormous variability in terms of habitats and social systems (Goodwin, 1986; Hanlon and Messenger, 2018). Corvids are found on all continents (except Antarctica) and in habitats as different as hot deserts and glaciers, with some species inhabiting astonishing diverse regions. For instance, the common raven (*Corvus corax*) can be found from Siberia to North Africa, and from Central America to Alaska. Social systems in corvids span from territorial pairs as in the Eurasian jays (*Garrulus glandarius*), and small family groups with non-breeding helpers as in Florida scrub-jays (*Aphelocoma coerulescens*), to large colonies as in rooks (Clayton and Emery, 2007). Further, individuals show great flexibility such that social systems may vary among different populations (Baglione et al., 2002), as well as during the ontogeny (Boucherie et al., 2019). In a similar vein, cephalopods can be found in all marine habitats, from shallow waters to ocean depths and from tropical to polar region. Some species have remarkably large geographic distribution such as the common octopus (*Octopus vulgaris*), which is found in the Mediterranean, Atlantic, Caribbean, and Japan seas. Further, social systems in cephalopods span from tendentially strict solitary life styles in octopuses, to breeding aggregation in some cuttlefish and up to gregarious schooling in squids (Schnell and Clayton, 2019). As result of the great speciousness and socioecological variability, the study of corvids and cephalopods can allow wide correlation analyses between proxies of intelligence and socioecological features, and thus a powerful testing of the main hypotheses for the evolution of intelligence.

In the remaining part of this chapter I will review the current state of art in regard to the evolution of intelligence in corvids and cephalopods. By adopting Seed (2007)'s framework, I will subsequently discuss at what level of analysis corvids' and apes' cognition may have evolved convergently on the basis of the evidence available. In parallel I shall use the same approach to compare cephalopods with large-brained vertebrates. Finally, I will highlight key research gaps in each group, and outline how, by addressing these issues, this thesis will attempt at fostering a deeper level of understating of convergent cognitive evolution in corvids and cephalopods.

1.5: CORVIDS' COGNITIVE EVOLUTION

How complex is corvid cognition?

Indications that corvids may be endowed with complex cognition comes both from neuroanatomical and behavioural proxies. In regard to the former, corvids' encephalization quotient is comparable to that of great apes and higher than that of any other group of birds (except from parrots; Emery, 2006; Jerison, 1973). In addition, as in apes, brain regions that are thought to be involved in complex cognition (i.e. nidopallium and mesopallium) are particularly enlarged in corvids (Rehkämper et al., 1991; Sayol et al., 2016). In regard to the latter, a number of experiments have reported high levels of behavioural flexibility and provided evidence that cognition in corvids – as in apes – may involve mechanisms more complex than hardwired predispositions and associative learning. Due to the large amount of literature, I will not attempt to provide a comprehensive review of the topic. Rather, in what follows I wish to highlight what are in my view the most remarkable examples of behavioural evidence of complex cognition in corvids and apes. The reader may refer to the work of other authors for recent reviews (Clayton and Emery, 2015; Krupenye and Call, 2019; Taylor, 2014).

One cognitive domain in which at least some corvids appear to be on par with apes is physical problem solving. Empirical evidence indicates that, similarly to apes (Bania et al., 2009; Martin-Ordas et al., 2012; Mulcahy et al., 2005), New Caledonian crows (*Corvus moneduloides*) and rooks (*Corvus frugilegus*) spontaneously choose and manufacture appropriate tools for a specific task, use tools to gain access to other objects that can in turn be used to acquire food (sequential tool use), and flexibly use multiple tools and/or strategies to solve similar tasks (Auersperg et al., 2011; Bird and Emery, 2009; Chappell and Kacelnik, 2002; Taylor et al., 2007). Further, these two species of corvids appear to rival great apes in solving trap-tube problems. In the classic version of the task, animals have to insert a stick in a clear horizontal tube and to push a bait outside the apparatus by avoiding a trap (a hole sealed on the bottom side and located in the middle part of the tube; Visalberghi and Limongelli, 1994). The performance of apes and corvids in a variety of modified version of this task suggests that both groups are capable of solving such problems through some level of causal understanding (Mulcahy and Call, 2006b; Seed et al., 2006, 2009b; Taylor et al., 2009).

A number of studies have also suggested that corvids and apes may share the ability to plan for the future[5], namely that they may recall specific features of a past episode and act in the present to meet future motivational states. This capability is thought to be based on the same cognitive machinery involved in episodic-like memory (Clayton et al., 2003; Suddendorf and Corballis, 2007), i.e. a process allowing to remember the what-where-when feature of a past episode, which has been demonstrated in both corvids (Clayton and Dickinson, 1998) and apes (Martin-Ordas et al., 2010). The most compelling evidence that corvids may be able to plan for the future comes from caching experiments in jays (California scrub-jays: Correia et al., 2007; Raby et al., 2007; Eurasian jays: Cheke and Clayton, 2012). In the most recent study, Cheke & Clayton (2012) tested jays' capability to plan for the future with a paradigm that relied on specific satiety, a phenomenon in which individuals experience a reduction of desire toward a specific kind of food as a result of having been fed that food to satiety (Balleine and Dickinson, 1998; Dickinson and Balleine, 1994). The experiment encompassed three trials, with each trial being formed by three stages. In trial 1 (stage 1), jays were presented with maintenance food and then allowed to cache food A and food B in two possible locations (location 1 and 2). A few hours later (stage 2), jays could eat one food to satiety (e.g. food A) and then retrieve the items that were cached in stage 1, but only from location 1. Finally, on the following day, jays could feed on the alternate food (e.g. food B) before having the possibility to retrieve items from the other location (e.g. location 2). Trials 2 and 3 were identical with the exception that food A or food B were provided in stage 1 rather than maintenance food. The authors found that on the first trial, jays cached the two kinds of food in similar proportions across the two locations. In later trials however, birds adjusted their caching pattern: jays tended to accumulate a given food in a specific location (e.g. food B in location 1) such that in stage 2 and 3 they could retrieve the most desired food, i.e. the food they were not sated on at the time of recovery. Thus, results of this experiment are consistent with the possibility that Eurasian jays can perform an action in the present to meet a future motivational state (e.g. desire for a specific food) that is conflicting with the current motivational state. On the other hand, future planning in apes has been mainly tested in the context of tool use. For instance, Osvath and Osvath (2008) showed that chimpanzees and orang-utans select a tool over an immediate reward to gain access to more valuable reward in the future. Additional evidence also suggests that apes may save tools for the future to solve

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[5] Note that in the thesis I use 'prospection abilities' and 'future planning abilities' as synonymous.

experimental tasks (Mulcahy and Call, 2006a; but see Emery and Clayton, 2009), as well as spontaneously even without training (Osvath, 2009a).

Another domain in which remarkable performance of both apes and corvids were reported is social cognition. Current evidence is consistent with the possibility that these animals may respond to the mental states of a conspecific, such as perspectives, desires, knowledge and beliefs (Theory of Mind). In regard to perspectives, multiple studies indicate that apes may take into account what others can see and hear to maximize individual benefits (Bräuer et al., 2007; Karg et al., 2015a; Melis et al., 2006). For instance, Melis et al. (2006) found that chimpanzees tend to reach for a reward through an opaque or a silent tunnel in the presence of a human competitor but show no preference between clear-opaque and silent-noisy tunnels when alone. In a similar vein, California scrub-jays (*Aphelocoma californica*) and Eurasian jays appear to take into account the visual and acoustic perspective of others to minimize the risk of pilfering: they tend to cache in less visible locations (e.g. in the shadow, behind barriers, at distance) when observed by a conspecific, or in a non-noisy substrate when a conspecific cannot see but can hear them (Dally et al., 2005; Legg et al., 2016; Legg and Clayton, 2014; Shaw and Clayton, 2013; Stulp et al., 2009; for evidence in ravens see also Bugnyar et al., 2016). Interestingly enough, both scrub-jays and chimpanzees may also use self-experience to outperform competitors (Emery and Clayton, 2001; Karg et al., 2015b).

In regard to knowledge states, Kaminski et al. (2008) showed that chimpanzees distinguish between ignorant and informed conspecifics in a competitive task. Comparable evidence was reported in ravens (Bugnyar and Heinrich, 2005) and scrub-jays (Dally et al., 2006). In particular, Dally et al. (2006) found that if allowed to cache in the presence of a conspecific and subsequently allowed to recover their caches whilst the same individual is present, scrub-jays tend to re-cache selectively those items that were hidden in the sight of that individual, compared to the items that were previously cached in the view of a different conspecific.

Flexible social cognition in both groups however is not restricted to competitive scenarios. When sharing food with their mate, male Eurasian jays select the food according to the specific satiety of the females, thus suggesting they may be able to attribute desires to conspecifics (Ostojić et al., 2013, 2014, 2016). On the other hand, Buttelmann et al. (2017) presented apes with an active helping paradigm, providing some indication that apes' sensitivity to beliefs may not be only implicit (Krupenye et al., 2016), but it can also translate into actions.

Evolutionary pressures

According to the Ecological Intelligence Hypothesis, three factors may have played a key role in the evolution of intelligence: generalist diets, extractive foraging (particularly with tools) and spatio-temporal dispersed resources (Byrne, 1997; Milton, 1981; Parker and Gibson, 1977). Were these factors relevant in the evolution of corvids? Most corvids are highly omnivorous, feeding on fruits, berries, insects, eggs, and even vertebrates (e.g. reptiles, small birds and mammals; Goodwin, 1986). Further, these birds employ various extractive foraging techniques, often requiring the concerted actions of feet and beak (Goodwin, 1951). For instance, rooks dig in the soil for roots and invertebrates (Lockie, 1956), while Eurasian jays and carrion crows crack open nuts and mussels, respectively (Goodwin, 1951; Whiteley et al., 1990). New Caledonian crows and Hawaiian crows (*Corvus hawaiiensis*) routinely use tools during foraging (Rutz et al., 2010, 2016). The former, which have been studied in more detail, manufacture different kinds of tools: hook-like tools are fashioned from twigs/leaves to extract insects from cervices, whereas stepped-cut tools are obtained from Pandanus leaves and used to probe for prey under leafy detritus (Hunt, 1996; Hunt and Gray, 2004a, 2004b). However, despite sporadic reports existing for other species (Boire et al., 2002), tool-mediated foraging is not widespread within corvids. Given that multiple species of corvids can develop tool use behaviour in captivity despite not habitually using tools in the wild (e.g. rooks, Bird and Emery, 2009; Eurasian jays, Cheke et al., 2011; California scrub-jays, Logan et al., 2016), these data are unlikely to be explained by the lack of cognitive capacity for using tools. Rather, the rarity of tool-mediated foraging in corvids may stem from the constraints and opportunities set by their morphology. By lacking grasping hands and ape-like physical strength, corvids may have limited opportunity to use tools when compared to apes (Seed et al., 2009a). In parallel, corvids' beak may act as an in-built tool for certain tasks (e.g. to dig in the soil), such that tool-use may more rarely confer benefits to corvids than to apes (Seed et al., 2009a). If this is the case then tool-mediated foraging may not have been as crucial as a factor in the evolution of corvids as it has been proposed in the case of primates.

Finally, corvids rely substantially on spatio-temporally dispersed resources. With a few exceptions, these birds are food hoarders, hiding food for later consumption (de

Kort and Clayton, 2006). Specialized cachers (e.g. most jays) hide large amount of staple food (up to 33000 items/year in Clark's nutcrackers; Kamil and Balda, 1985) in periods of seasonal abundance and retrieve them during the harsher time of the year. On the other hand, moderate cachers (e.g. crows, ravens) hoard a variety of food types (including perishable items, e.g. insects) throughout the year but never depend on cache retrieval for surviving. Caching may pose important cognitive challenges particularly in the case of moderate cachers who hide foods that degrade at different rates. The need to integrate information about what food was cached when and in which location may have selected for episodic-like memory and perhaps future planning abilities (Grodzinski and Clayton, 2010). Since the ancestor of corvids was likely to be a moderate cacher (de Kort and Clayton, 2006), such cognitive adaptations may have evolved in the corvids' ancestor, such that they may be widespread among extant species. Therefore, the ecological challenges of caching may be comparable to those experienced by primates feeding on tropical ripe fruits (Seed et al., 2009a).

In contrast, the Social Intelligence Hypothesis posits that cognitive sophistication evolves for competing, cooperating and acquiring information from others. Thus, cognition is considered as an adaptation for navigating complex social environments (Byrne, 2018; Whiten and van de Waal, 2017). Were these selective pressures relevant in the evolution of corvids?

When group size is used as a proxy for social complexity, birds violate the prediction of the Social Intelligence Hypothesis: brain size does not correlate with group size; rather long-term monogamous species have the larger brains (Beauchamp and Fernández-Juricic, 1999; Emery et al., 2007; Shultz and Dunbar, 2007). However, it has been argued that these data do not reflect the lack of relevance of social pressure in birds' cognitive evolution. The fact that brain size positively correlates with long-term monogamy in birds – rather than with group size as in primates – may result from key differences in reproductive biology and, consequently, social system between birds and mammals. Parental investment is remarkably more skewed toward females in mammals than in birds, particularly for avian species raising altricial offspring, which typically requires bi-parental cares (Orians, 1969; Sibly et al., 2012). According to Emery et al. (2007) this biological difference between groups has important implications in term of cognitive challenges faced by birds and mammals within bonds with pair mates. Specifically, long-term monogamous birds need to maintain enduring and cooperative relationships that may pose challenges comparable to those experienced by primates in their bonds with multiple members of the group. Evidence from corvids supports this idea. For instance, rook pair-mates – who pair for life and raise altricial chicks – exhibit high levels of cooperation (e.g. nest building, offspring feeding, predator defence), synchronization, affiliative behaviour (e.g. food sharing, allopreening), and third-party affiliations (Emery et al., 2007; Seed et al., 2007). Others however have argued that the complexity of monogamous relationships in corvids does not cover the whole story. It is common for juvenile corvids to join mixed-sexes, temporary flocks during a number of years before forming breeding pairs (Goodwin, 1986). Evidence in ravens indicates that these 'juvenile societies' resemble primates' fission-fusion groups, requiring the birds to keep track of individual ranks, build alliances, acquire information form others (e.g. food location) and maintain 'friendships' (Boucherie et al., 2019; Braun and Bugnyar, 2012; Loretto et al., 2012). Thus, during a limited ontogenetic stage, corvids and primates may share quite similar social challenges.

An additional factor that is thought to have played a key role in corvids' cognitive evolution is caching. Due to the evidence of seemingly complex cognition expressed by corvids in the caching context (e.g. Cheke and Clayton, 2012; Dally et al., 2006), and because of the ecological relevance of food hoarding in this group, it appears plausible that a cognitive arms race between cachers and pilferers may have elicited complex sophistication to maximized the benefits of both players (Bugnyar and Kotrschal, 2002; Dally et al., 2005; Grodzinski and Clayton, 2010).

Finally, with regard to social learning, a number of studies indicate that corvids rely on the vicarious acquisition of information in the wild. For instance, jackdaws are more likely to consume novel foods after witnessing a conspecific feeding on that food (Greggor et al., 2016), while American crows learn to recognize novel threats from peers (horizontal transmission) and from parents (vertical transmission; Cornell et al., 2012). Further, social learning is involved in the development of tool manufacture in New Caledonian crows (Kenward et al., 2006), a set of behaviours that appear to vary across populations as a result of cultural processes (Hunt and Gray, 2003). However, the number of behavioural traditions reported in corvids is not comparable to those observed among primates, such that it is not clear whether social learning played a crucial role in corvids' evolution as it has been proposed for primates.

In sum, corvids face a number of socioecological challenges that, although not identical to those experienced by primates, appear to be of comparable difficulty.

Level of convergence

Based on these pieces of evidence, to what extent can we consider corvids to be akin to 'feathered apes' (Emery, 2004)? More specifically, at what level of analysis can corvids' and apes' cognition be said to have converged? Current evidence may provide sufficient grounds to support the idea that corvids and apes may have converged at the second level of analysis. Specifically, these groups may not just perform comparably complex and flexible behaviours (first level); they may also share cognitive underpinnings that are to some extent more complex than hardwired predispositions and associative learning (second level)[6]. What about the third and deeper level of convergence? In an influential paper, Emery and Clayton (2004) hypothesized that corvids and apes may have independently evolved a similar cognitive-tool kit encompassing four mental pillars: causal reasoning, flexibility, imagination and prospection. In my view, there are two main issues that currently impair a satisfactory evaluation of this idea. The first concerns a systemic problem in the field of comparative cognition. As mentioned earlier – due to the lack of a solid description and formalization of intelligence – complex cognitive processes tend to be invoked through a process of exclusion of simpler mechanisms. As a result, it is currently challenging to test whether different lineages, such as corvids and apes, may also have converged at the third level of analysis, namely that similar cognitive processes may underlie their flexible behaviour. The second problem is more specifically related to corvids, and it more likely reflects the fact that this group encompasses a substantially larger number of species and it is a far more recent model for the study of cognition than apes. As noted by Seed (2007), despite evidence of complex cognition being available for both apes and corvids, in the case of the former such evidence results from a systematic investigation of different cognitive domains in the same species, with chimpanzees being the most notable example. In contrast, evidence of complex cognition in corvids is more spread within the family, with some cognitive abilities being investigated predominantly/exclusively in a small subset of species. For instance, the idea that corvids are excellent physical problem solvers hinges predominantly on the study of the *Corvus* genus (e.g. New Caledonian crows, rooks),

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[6] Note however that a number of alternative explanations have proposed to interpret the experimental evidence of apparently complex cognition for both corvids and apes (e.g., Problem solving: Ghirlanda and Lind, 2017; Hennefield et al., 2018; Penn and Povinelli, 2007a; social cognition: Heyes, 2015, 2017; Penn and Povinelli, 2007b; future planning: Lind, 2018; Suddendorf and Corballis, 2007). As result, it is still a matter of dispute whether corvids and apes are capable of cognitive processes that are more complex than associative learning and hardwired predisposition.

whereas the notion that corvids are capable of planning for the future mainly relies on the study of California scrub-jays and Eurasian jays. This is not to say that the species/genus of corvids mentioned above have never been tested in other cognitive domains, or that physical cognition and prospection abilities have never been sampled in other corvid species. Yet, such studies are rarer and sometimes failed to provide convincing support for complex cognition. For example, California scrub-jays performed poorly in a series of tool use experiments (Logan et al., 2016) and string pulling tasks (Hofmann et al., 2016). Further, the recent evidence that ravens (another member of the *Corvus* genus) can plan in the context of tool use and bartering (Kabadayi and Osvath 2017) has been challenged (Lind, 2018; Redshaw et al., 2017), such that solid conclusion on prospection abilities in the *Corvus* genus, or in corvid species other than California scrub-jays and Eurasian jays, cannot be drawn. Therefore, while claims about a cognitive tool-kit in apes can be abstracted from (relatively) complete investigations of the different abilities in question within each species, current claims of a cognitive tool-kit in corvids are based on partial investigations where different cognitive abilities are assessed in different species/genera. As such, it is currently not clear whether the remarkable cognitive complexity observed at the level of the corvid family results from complementary cognitive specializations in different subgroups, or from a domain general cognitive tool-kit shared by individual species of the corvid family as hypothesized by Emery & Clayton (2004; cf. Seed 2007).

A useful approach to clarify this issue is to conduct a systematic investigation of different cognitive domains in a single species of corvids. This multifaceted testing of cognitive complexity in one species will foster insights into whether corvids are indeed endowed with a domain general cognitive-tool kit, thus ultimately facilitating the study of convergent cognitive evolution between corvids and apes, at a deeper level of analysis. The first objective of this thesis will be to adopt such an approach to the study of the Eurasian jay, a corvid species for which some indication of complex complexity has been reported. To this end, I will attempt to fill the gap in our current knowledge by probing into problem solving, future planning and social cognition abilities of these jays.

1.6: THE EURASIAN JAY

Socioecology

The Eurasian jay (*Garrulus glandarius*; Fig. 1.3) is a species of corvids inhabiting woodlands and copses across vast geographic regions, from Scandinavia to North Africa, and from Russia to Eastern Asia. Like most corvids, these jays have an omnivorous diet, which includes insects, berries, fruits, eggs, young birds, and other small vertebrates (e.g. mice, lizards; Goodwin, 1986). However, acorns are usually a staple food. The Eurasian jay is a specialized cacher who hoards nuts in large quantities during autumn and then retrieves hidden food during the harsh winter season (Bossema, 1979; de Kort and Clayton, 2006). Cached items are protected from pilferers (both conspecifics and heterospecifics) through aggressive displays, or by displacing the items to novel locations (Bossema, 1979; Goodwin, 1951). Eurasian jays form cooperative monogamous pairs, with both parents engaging in nest building and feeding of chicks, and with males feeding the females before and during incubation (Clayton and Emery, 2007; Goodwin, 1986). During breeding season, pairs typically occupy non-overlapping territories which are actively defended, whereas individuals appear more tolerant to the presence of conspecifics (e.g. neighbours) at other times of the year (Grahn, 1990). In contrast to other species of corvids (e.g. raven), Eurasian jays do not form large flocks, neither before nor after reaching sexual maturity (Grahn, 1990).

Figure 1.3: An Eurasian jay (*Garrulus glandarius*) sitting on a branch (Credit: Charlie Jackson)

Cognition: what we do and do not know

To date, different aspects of Eurasian jay cognition have been investigated (Tab. 1.1). Yet a number of issues remain unexplored and/or appear in need of further clarification (Tab. 1.1). In what follows I shall summarize the available literature and unanswered key questions.

With regard to physical cognition, these jays have been used as a model in developmental studies of object permanence (Zucca et al., 2007) and causal relationships between objects (e.g. support intuition; Davidson et al., 2017). To the best of my knowledge, only two studies have been published on physical problem solving in Eurasian jays (Cheke et al., 2011; Miller et al., 2016). Interestingly, both studies showed that – although these jays are not known for using tools in the wild – they can develop (learn) tool use behaviours in captivity. Cheke et al. (2011) first trained jays to solve an object-dropping task: birds had to learn to insert a tool (e.g. a stone) into a vertical tube, an action that provided access to a food reward placed inside the apparatus. Subsequently, jays were presented with a variety of tasks requiring them to select a functional tool or apparatus. For instance, in one experiment jays were presented with a liquid-filled apparatus in which a floating reward was placed. Birds had to choose between inserting sinking objects or floating objects, with the former being the functional tool, i.e. only sinking objects would cause the level of liquid into the tube to rise, thus making the floating reward reachable. The performance of Eurasian jays in this test indicated that jays could learn a preference toward functional sinking tools. More in general, across all the experiments, performance suggested that tool use behaviour in this species relied on the interplay between instrumental learning and causal understanding. More recently, Miller et al. (2016) investigated if these jays could learn to solve an object-dropping task by observing a conspecific. The study failed to find evidence that Eurasian jays can socially learn to use tools; however, it corroborated the result that tool use behaviour can emerge through training. Building on this evidence, a number of experimental questions that have already been addressed in other species of corvids can be investigated in Eurasian jays. Can these jays select functional tools according to other physical properties, such as size and shape? Are these jays capable of flexibly using different kinds of tools and/or different strategies to solve a similar task? Can these jays use sticks as tools?

With regard to future planning abilities, a single study has been conducted in Eurasian jays. Cheke and Clayton (2012)'s experiment, which I have described previously, is often acknowledged as one of the most convincing piece of evidence that corvids, or perhaps non-human animals, may be able to plan for the future (Shettleworth, 2010). However, alternative explanations that do not involve planning have been proposed to interpret corvids' performances in future planning experiments (e.g. Dickinson, 2011). For instance, one hypothesis – which I will refer to as the 'Compensatory Caching Hypothesis' – suggests that jays may be endowed with a natural propensity to distribute resources uniformly, thereby hoarding items in areas where food was not available in past, or caching a given type of food in locations in which that specific food was not previously experienced (Premack, 2007; Suddendorf and Corballis, 2008). This valuable lower level explanation for apparent future planning abilities of corvids in the caching context, still need to be tested empirically. The Eurasian jay is an ideal model species to investigate the Compensatory Caching Hypothesis, albeit this alternative interpretation was not formulated to address specifically the results obtained by Cheke and Clayton (2012).

Table 1.1: Summary of the main findings and open questions (yellow cells) with regard to the physical problem solving, future planning, and social cognition abilities of the Eurasian jay (Ej).

Domain	Reported Effects & Open Questions	References
Physical Problem Solving	Learn to use tools (object dropping tasks) through training	Cheke et al. 2011; Miller et al. 2016
	Learn to select functional tool based on density	Cheke et al. 2011
	Can Ej select functional tools according to the size and shape of objects?	
	Can Ej use sticks as tools?	
Future Planning	Distribute caches to maximize future benefit, in line with planning abilities	Checke and Clayton 2012
	Is future-oriented caching in Ej underpinned by predispositions or prospection abilities?	
Social Cognition	Protect caches by responding to the visual perspective of a conspecific	Legg and Clayton 2014
	Protect caches by responding to the acoustic perspective of a conspecific	Shaw and Clayton 2013
	Protect caches by responding to the current desire of a conspecific	Ostojic et al. 2017
	Adjust food sharing by responding to the current desire of the pair mate	Ostojic et al. 2013, 2014, 2016
	Can Ej integrate cues about others' desires and perspectives to protect their caches?	

Finally, social cognition is the area of cognition on which Eurasian jays' research has been focusing more intensively. As mentioned earlier, caching experiments indicate that these jays may be sensitive to the visual and acoustic perspective of conspecifics (Legg and Clayton, 2014; Shaw and Clayton, 2013), while food sharing experiments suggest that they may take into account another agent's desire (Ostojić et al., 2013, 2014, 2016). Recently however, Ostojić et al. (2017) showed that Eurasian jays may also take into account another bird's desire to protect their caches, although this may have been achieved by responding to the conspecific' behaviour, without the need to consider others' mental states. Building on this, it would be particularly interesting to ask whether jays – like humans – are capable of taking into account different mental states (or behavioural cues correlating with mental states) simultaneously. For instance, can jay integrate others' desire and perspective? These questions will be empirically investigated in this thesis in order to gain further insight into the cognitive complexity of problem solving, future planning and social cognition in the Eurasian jay.

1.7: CEPHALOPODS' COGNITIVE EVOLUTION

How complex is cephalopods' cognition?

Coleoid cephalopods are endowed with a remarkably complex brain that resembles that of some vertebrates in size (corrected for body size; Packard, 1972) and in density of interneuron connections (Young, 1991, 1995). Among the various ganglia that constitute the cephalopod brain, the vertical lobe – which plays a pivotal role in learning and memory (Fiorito and Chichery, 1995; Shomrat et al., 2015) – has been compared to regions of the mammalian cortex and avian nidopallium (Edelman and Seth, 2009; Young, 1995). Cephalopods also exhibit rich and flexible behavioural repertoires. For instance, octopuses use a variety of solid objects (e.g. stones, shells) and even water, as tools for different purposes (Finn et al., 2009; Mather, 2016), whereas many species, particularly among cuttlefish and squid, appear to employ flexible mating tactics (Brown et al., 2012; Moynihan and Rodaniche, 1982; Schnell and Clayton, 2019) and anti-predatory strategies (Langridge et al., 2007; Staudinger et al., 2011, 2013b). To date, however, the cognitive mechanisms underpinning cephalopods' behaviour are still largely unexplored. Hence, it is not clear whether the behavioural flexibility exhibited by this groups is actually the expression of complex cognitive abilities. Nevertheless, some intriguing evidence supporting the idea that cephalopods may be endowed with a vertebrate-like cognitive complexity is available. A study by Jozet-Alves et al. (2013) indicated that cuttlefish – like corvids – may possess episodic-like memory. Given that this form of memory is thought to be based on the same cognitive machinery required to plan for the future (Clayton et al., 2003; Suddendorf and Corballis, 2007), results of this study raise the possibility that cephalopods may also have prospective cognition (see also Billard et al., 2020). More recently, Yang and Chiao (2016) found that number discrimination skills in cuttlefish are comparable to those of primates, and may involve an analogous mechanism of numerical representation. Further, this study also showed that quality discrimination in cuttlefish is influenced by the hunger state, akin to economic decision making in humans (Yang and Chiao, 2016). Another interesting line of evidence concerns problem solving in octopus. Richter et al. (2016) presented octopuses with a series of tasks requiring the animals to retrieve a baited L-shaped food container. Octopuses appeared not to rely on simple learning mechanisms to solve the tasks, instead they seemed to employ flexible and potentially more cognitively complex strategies.

Evolutionary pressures

The evolution of cephalopods has been attracting the interest of scientists for decades. This topic however has been traditionally investigated with a focus on sophisticated biological and physiological traits such as the camera eye, suckered arms, dynamic colour skins, and buoyancy mechanisms (Messenger, 2001; Packard, 1972; Voight et al., 1995). These adaptations, as well as complex behaviours, are thought to have evolved as a result of the competition and predation exerted by marine vertebrates (Hanlon and Messenger, 2018; Packard, 1972). The study of cognitive evolution in cephalopods has received far less attention. In a popular science book, Godfrey-Smith (2016) recently suggested that ecological challenges (e.g. extractive foraging, generalist diets) may have played a role in the evolution of cephalopods' cognition. Nevertheless, the relevance of the main hypotheses for the evolution of intelligence has not yet been properly evaluated in this group. As a result, it is currently unclear whether similar evolutionary pressures may have elicited the emergence of large brains and behavioural flexibility in cephalopods and in the main groups of intelligent vertebrates.

Level of convergence

Mather and Dickel (2017) provocatively suggested that cephalopods may share with corvids and apes a cognitive tool-kit hinging on causal reasoning, flexibility, imagination and prospection. Thus, according to the authors, cephalopods may have converged with large brained vertebrates at the deepest level of analysis, i.e. behavioural flexibility in these groups may be underpinned by similar cognitive processes. In my view, this is idea is currently highly speculative. This is because current indications of cognitive complexity in cephalopods are still quite preliminary. Further, given the key differences in sociality and life history between cephalopods and intelligent vertebrates, it is not clear whether the same evolutionary pressures may have shaped the evolution of these groups. Specifically, cephalopods have fast life histories (e.g. life spans shorter than two years, no parental care, a single reproductive event; Rocha et al., 2001), and do not appear to engage in complex social bonds, even in the case of the highly social squids (Boal, 1996; Schnell and Clayton, 2019).

It will be the second objective of this thesis to lay the groundwork for studying convergent cognitive evolution between cephalopods and large-brained vertebrates. By reviewing current indications of behavioural flexibility in cephalopods I will first evaluate whether the available evidence is sufficient to support a case of behavioural convergence (first level of analysis) among these groups. Subsequently I will attempt at devising an evolutionary hypothesis for the emergence of large brains and behavioural flexibility in cephalopods. Finally, I will propose novel behavioural paradigms that may allow to explore the cognitive underpinning cephalopods' complex behaviours.

1.8: THESIS OVERVIEW

In summary, a number of distantly related lineages may have evolved intelligence independently from primates. Among these groups, the corvids and the cephalopods represent two particularly interesting cases. With regard to the corvids, current evidence supports the idea that cognitive abilities more complex than hardwired predispositions and associative processes may have evolved convergently in corvids and apes, in response to comparable socioecological pressures. However, further research is needed to evaluate whether convergent cognitive evolution between these two groups may have occurred at a deeper level of analysis (e.g. Seed 2009a; Seed et al., 2007), namely if a similar cognitive tool-kit underpins behavioural flexibility in both corvids and apes (Emery and Clayton, 2004). A key factor constraining the evaluation of this hypothesis is that evidence of cognitive sophistication in different domains is not currently available *within* the same species of corvids. Hence it is not possible to distinguish whether the apparent domain general cognitive complexity of corvids is the expression of similar cognitive abilities shared by individual members of the corvid family, or rather whether it is the result of complementary cognitive specializations among different subgroups.

As for the cephalopods, preliminary evidence is consistent with the possibility that these molluscs may have independently evolved large brains and behavioural flexibility that are to some extent comparable to those of vertebrates. Yet, because the study of the cognitive evolution in cephalopods is very young, it is not yet clear how complex their cognition is, nor which pressures may have been responsible for their cognitive evolution. As a result, very little can be said about the level at which they may have converged with intelligent vertebrates.

The general aim of this thesis is to gain further insights into the process of convergent cognitive evolution. My first objective is to take one step further in understanding how deep the cognitive convergence between corvids and apes may be. To this end I will report four empirical studies exploring cognitive complexity among different domains in a single species of corvids, the Eurasian jay. My second objective is to investigate the potentials of cephalopods as a novel model group for the study of convergent cognitive evolution. I will attempt at laying both theoretical and methodological groundwork for testing these fascinating molluscs. This dissertation is therefore divided into two parts: in Chapters 2-5 I will focus on corvids, whereas in Chapter 6 I will turn my attention to the cephalopods.

To begin addressing the first objective, **Chapter 2** focuses on tool use abilities in Eurasian jays. Previous research has suggested that these jays may learn a preference toward functional sinking tools (over floating tools) to solve water-displacement tasks (Cheke et al., 2011). Through two tool selectivity tests, this chapter explores whether Eurasian jays can select appropriate tools according to other physical properties, namely size and shape. Additionally, jays' capability of using novel tools (sticks) to solve a task with a familiar apparatus is also evaluated. In contrast to fellow corvids (e.g. rooks; Bird and Emery, 2009), jays could not spontaneously adjust their selection according to the functionality of the tools, thus suggesting that they may be endowed with more limited tool selectivity abilities. Yet, supporting previous findings in this species, jays' performance indicates they are able to modify their tool use behaviour through learning. When presented with sticks, jays could use these novel objects to acquire food rewards from a familiar apparatus, a finding which represents the first evidence that Eurasian jays are capable of using sticks as tools.

Chapter 3 further investigates complex cognition in Eurasian jays by focusing on future planning abilities. Caching experiments in jays are often regarded one of the most convincing piece of evidence that non-human animals may be able to plan for the future. However, alternative explanations accounting for jays' performances in these studies have been proposed, although these have to date never been empirically tested. For instance, the Compensatory Caching Hypothesis suggests that jays' apparent future planning behaviour is instead the expression of a natural propensity to distribute resources uniformly. In this chapter, I report a novel paradigm that was designed to test the hypothesis that jays are capable of future planning against the Compensatory Caching Hypothesis. Interestingly, jays' performance did not provide support for either of the two contrasting hypotheses, thus challenging both alternative accounts.

Social cognition is the domain that has been more intensively investigated in the Eurasian jay. Previous research found that these jays employ flexible anti-pilfering strategies, thereby minimizing the risk of cache loss by responding to the visual perspective (Legg and Clayton, 2014) or the desire toward specific food of a conspecific (Ostojić et al., 2017). Building on this work, **Chapter 4** investigates whether Eurasian jays are capable of integrating information about another bird's visual perspective and desire to most effectively protect their caches. Across two experiments, jays' caching pattern consistently provided no evidence that they can integrate multiple social information. However, these results could not support previously reported effects either: jays' performance did not show that these birds can adjust their caching behaviour by responding to a single social cue (either to the visual perspective or the desire of another bird). This finding is surprising considering that the procedures employed in these experiments closely matched those previously used by Legg and Clayton (2014) and by Ostojić et al. (2017) to show, respectively, that Eurasian jays respond to others' visual perspective and desire in the caching context.

To further explore this unexpected outcome, **Chapter 5** investigates the reliability of the two original effects, independently. In one experiment I conduct a replication of Legg and Clayton (2014)'s study and find that jays did not tend to cache behind an opaque barrier in the presence of a conspecific. This result is in line with the outcomes of the previous chapter, which shows that jays could not adjust their caching behaviour according to the visual perspective of a conspecific. In a second experiment, I test whether a minor difference in set-up between the experiments conducted in Chapter 3 and in Ostojić et al. (2017)'s study – i.e. the presence/absence of a clear barrier – could have influenced jays' capability to respond to the desire of conspecifics across the studies. Consistently between the two slightly different set-ups, jays exhibit a caching pattern that does not support their ability to respond to another bird's desire, thus further corroborating the results of the previous chapter. Taken together, these two experiments appear to put into question the reliability and robustness of the effects reported in the original studies.

In **Chapter 6** I turn my attention to the cephalopods. I first review the most relevant cases of behavioural flexibility in this group. I suggest that current evidence appears solid enough to hypothesize that cephalopods and large-brained vertebrates may have converged at the behavioural level (i.e. first level of analysis). Subsequently, I outline a hypothesis for the evolution of cognition in this group, in relation to the main hypotheses discussed for vertebrates. Additionally, I present a number of novel experimental paradigms to test cephalopods' cognitive underpinnings in different domains.

Finally, in **Chapter 7** I summarize the main outcomes of my empirical studies in the Eurasian jay, and my theoretical and methodological study in cephalopods. Relating back to the two objectives of this thesis, I discuss the implications of my findings. Specifically, I consider whether the hypothesis that corvids are endowed with a domain-general cognitive tool-kit is supported in the Eurasian jay, and evaluate the potentials of cephalopods as a novel model group for the study of convergent cognitive evolution. I conclude by outlining future research avenues that may deepen our current understanding of corvids' and cephalopods' cognitive evolution.

CHAPTER 2[7]:

How flexible is tool use in Eurasian jays?

Abstract

Eurasian jays have not been reported to use tools in the wild, yet they can be trained to solve object-dropping tasks, i.e. to insert a tool into an apparatus to release a food reward. Previous research suggests the these jays can learn a preference toward functional tools – objects allowing to obtain a food reward placed inside an apparatus – according to their density (Cheke et al., 2011). However, it is not yet known whether they can also select functional tools (tool selectivity) according to other physical properties such as size and shape, and use different kinds of tools to solve a similar task. In this chapter I conducted three object-dropping experiments aimed at exploring these abilities in Eurasian jays. In Experiment 2.1, jays tended to select large stones as tools irrespective of the diameter of the apparatus. However, jays progressively developed a preference for the small tool, which was functional with both the wide and the narrow apparatuses. In Experiment 2.2, only vertically-oriented long stones could fit into the narrow apparatus, whereas both long and round stones were functional with the wide apparatus. Jays showed a preference for the long stone and, with the narrow apparatus, tended to achieve the correct manipulation after one or more unsuccessful attempts. In Experiment 2.3, jays were able to use sticks and adopt a novel technique on the same object-dropping apparatus, thus providing the first evidence that Eurasian jays can use sticks as tools. Taken together, these results indicate that Eurasian jays may have limited tool selectivity abilities but nonetheless can use different kinds of tools to solve similar tasks.

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2.1: INTRODUCTION

In Chapter 1, I introduced corvids – a family of large brained birds thought to possess remarkable cognitive abilities (Emery and Clayton, 2004) – as an important model for studying the evolution of cognition in general, and convergent evolution in particular. The first objective of this thesis is to investigate to what extent different cognitive abilities reported across different corvid species can also be found within one species, the Eurasian jay. To begin addressing this objective, in this chapter I focus on one iconic expression of corvids' sophisticated cognition, namely their skill in solving physical problems by using tools.

The most prominent example of corvid tool use comes from the New Caledonian crow, a species considered to be among the most proficient tool users in the animal kingdom. These birds are, together with Hawaiian crows, the only corvid species currently known to develop tool use behaviours in the absence of training (Kenward et al., 2005; Klump et al., 2018; Rutz et al., 2016). Individual practice and social inputs, however, appear to be essential for juvenile New Caledonian crows to acquire some of the more complex tool behaviours habitually performed in the wild, such as the manufacture of hooked stick tools or stepped pandanus tools (Holzhaider et al., 2010; Kenward et al., 2006). Growing evidence indicates that, although relying on an inborn predisposition for manipulating objects (for a review see Amodio et al., 2018), tool use behaviours in New Caledonian crows may entail complex physical cognition. For instance, tool manufacture in these crows varies across populations and represents an example of behavioural tradition (Hunt & Gray, 2003) that, according to a recent study, may be sustained through a mechanism of mental template matching (Jelbert et al., 2018). Furthermore, studies in captivity indicate that New Caledonian crows may be capable of flexibly selecting functional tools by encoding relevant features of objects: these crows have been reported to select or manufacture tools of appropriate length to acquire out-of-reach baits (Chappell and Kacelnik, 2002; Knaebe et al., 2017), choose the most suitable raw materials (e.g. plant species) to shape hook tools (Klump et al., 2019), and distinguish between light and heavy objects by observing the movement of objects in the breeze (Jelbert et al., 2019). New Caledonian crows have also been found to build composite tools (von Bayern et al., 2018), solve sequential tool use tasks (Taylor et al., 2007; Wimpenny et al., 2009), and – when presented with a multi-access apparatus

– acquire food rewards by using up to four alternative strategies involving two different tools (i.e. sticks and balls; Auersperg et al., 2011).

Corvid species not known to habitually use tools in the wild also exhibit impressive skills in solving problems by using tools. Possibly the most famous case are rooks. Bird and Emery (2009) conducted a series of object-dropping experiments demonstrating that these birds are capable of tool selectivity: they can select functional tools based on their physical properties (e.g. size, shape). Rooks were presented with a set of tools differing in one feature (e.g. size) and with an object dropping apparatus, a transparent box with a baited, collapsible platform in the inside and a vertical tube on the top. To solve the task, birds had to select a functional tool (i.e. an object that could fit into the tube) and to drop it into the vertical tube of the apparatus, an action that would collapse the internal platform and thus release the food reward. In the size selectivity test, rooks could choose between three stones of different sizes. They were tested in two conditions: in the first half of the trials stones of all sizes were functional (*Wide tube* condition), whereas in the second half of trials only the small stones could fit into the apparatus (*Narrow tube* condition). Rooks were reported to have immediately switched their preference for large stones in the *Wide tube* condition to small stones in the *Narrow tube* condition. In the shape selectivity test, rooks were provided with two stones of different shapes and were again tested in the *Wide* and *Narrow* tube conditions. Rooks preferentially selected and correctly oriented long stones (over non-functional round stones) in the *Narrow tube* condition, in which only vertically-oriented long stones were functional (Bird and Emery, 2009). The authors found no evidence that rooks' preference toward tools of appropriate size and shape emerged through learning, such that birds may have spontaneously adjusted their selection on the basis of the feature determining whether or not tools were functional. In a follow-up test, Bird and Emery (2009) showed that rooks can acquire food rewards from the same apparatus by using sticks, i.e. tools that differed from the ones they have been trained with, and that required a different technique. Rooks dropped heavy sticks in the same way they had previously dropped the stones, but they adopted a distinct technique to solve the task with light sticks: they held the tool with their beak and pushed it downward to collapse the baited platform. Through a further set of experiments, Bird and Emery (2009) found that rooks are also capable of solving a sequential tool use task, as well as fashioning functional tools by removing side branches from twigs or shaping hook-like tools from straight wire.

Common ravens are another example of corvids that can use tools in captivity (e.g. Gallot and Gruber, 2019), although they do not habitually exhibit such behaviours in the wild. Kabadayi and Osvath (2017) recently reported that one raven successfully solved an object-dropping task on the first training trial, and subsequently employed an alternative tactic when stones were unavailable: the bird filled the apparatus with parts of the aviary floor, and thereafter pecked at the substrate when it came within reach (Kabadayi and Osvath, 2017). Although anecdotal, this observation suggests that ravens, like New Caledonian crows and rooks, may be capable of using different kinds of tools and devising alternative strategies to acquire food from the same apparatus.

The flexibility in tool-use behaviours reported in these studies appears to indicate that complex physical cognition may be widespread within the *Corvus* genus, a subgroup of corvids to which rooks, common ravens, New Caledonian crows and Hawaiian crows belong. Why tool use in the wild is only exhibited by New Caledonian crows and Hawaiian crows may be explained by a number of factors, including stronger inborn predispositions for manipulating tools (Amodio et al., 2018; Kenward et al., 2005, 2006), as well as idiosyncratic features of their habitats (e.g. reduced risk of predation, lack of extractive foraging competitors; Rutz and St Clair, 2012). As discussed in Chapter 1 however, it is not clear whether the sophisticated physical cognition reported in the *Corvus* genus is shared with more distantly related species of corvids. It has been shown that Eurasian jays and California scrub-jays can be trained to solve object-dropping tasks (Cheke et al., 2011; Logan et al., 2016; Miller et al., 2016). In the case of Eurasian jays, a member of the *Garrulus* genus, empirical evidence also suggests that these birds may take into account causal clues to solve tool use tasks. Cheke et al. (2011) presented Eurasian jays with a series of water displacement tasks that required the insertion of tools into an apparatus (i.e. a vertical tube filled with liquid) to acquire a reward, which could be reached only after the liquid has been progressively raised as a result of the insertion of the tools. In the study, the availability of causal cues was manipulated, such that in some tasks jays could choose between an apparatus or a tool that was functional according to physical principles and one that was not, whereas in other tasks jays had to select a functional apparatus according to arbitrary features such as colour, in the absence of available causal cues or when the available causal cues were counter-intuitive. Cheke et al. (2011) found that when causal cues were available, jays could learn to choose a functional liquid-filled apparatus over a non-liquid-filled apparatus containing only air or filled with a solid substrate, and learn to choose functional sinking tools over ones that float and therefore fail to raise the water level. When the functional apparatus could be identified on the basis of arbitrary features rather than on the basis of causal cues, jays could also learn to select the functional apparatus, but only in tasks in which the insertion of tools was ‘artificially’ (i.e. caused by the action of a hidden experimenter) associated with a progressive movement of the food reward. In contrast, jays failed to learn a preference toward the functional apparatus in a counter-intuitive task. When presented with a modified apparatus formed by one baited narrow tube and two non-baited wide tubes with different colour marks, jays could not learn to drop tools into the functional non-baited tube, an action that would raise the level of the liquid not only in the functional non-baited tube, but also in the adjacent baited tube because these tubes were invisibly connected. Thus, the overall performance of Eurasian jays in this study suggests that these corvids may have acquired tool use behaviours through an interplay between instrumental learning and causal understanding, with the latter fostering/constraining the learning process according to whether tasks fit or do not fit with physical principles (Cheke et al., 2011). Note, however, that recent meta-analyses of water displacement experiments in corvids have challenged the explanation that Eurasian jays’ and other species’ performance in these tasks may *also* have involved causal understanding to some degree, arguing instead that it may have been based *only* on simple learning and/or initial predispositions (Ghirlanda and Lind, 2017; Hennefield et al., 2018).

It is important to note that in the Cheke at al. (2011) study there are two confounding variables which may have affected jays’ performance in the task requiring jays to select functional sinking objects over non-functional floating objects. First, the two kinds of objects differed not only in density, the physical property that determined its functionality, but also in the material (rubber or foam) and colour (i.e. sinkable rubber pieces were either yellow or green, whereas floating foam pieces were either red, blue, yellow or green). Second, both individual birds that were tested had previous experience in dropping rubber tools, but not foam tools, in order to solve water displacement tasks. Specifically, both birds had taken part in a previous water displacement experiment in which rubbers and stones were provided as tools. Note however that the amount of their experience differed: one bird, Hoy, had used rubber on 35 occasions, whereas the other bird, Romero, had used rubber only once, and yet Hoy’s performance was no better than Romero’s. Nonetheless, it cannot be excluded that these jays developed a preference toward the functional rubber tool on the basis of trivial features (e.g. material) or due to a higher familiarity with these objects. Thus, it remains an open question whether Eurasian jays are capable – as rooks and New Caledonian crows – of selecting tools on the basis of an understanding of functionality.

To overcome these potential confounds and limitations, I conducted two tool selectivity tests in which functional and non-functional tools differed only in one feature (i.e. size in Experiment 2.1, and shape in Experiment 2.2), and were not familiar to the birds in the context of object dropping tasks. I presented the birds with two object dropping tasks that were designed after Bird and Emery's (2009) size and shape selectivity tests, and which involved an apparatus closely resembling that used in rooks. Finally, in a third experiment (Experiment 2.3) I explored jays' capability of using different tools – sticks – to acquire food for the same apparatus.

2.2: GENERAL METHODS

Subjects

Five hand-raised Eurasian jays of both sexes (three females and two males) were tested: Chinook, Homer, Jaylo, Poe, Stuka. At the time of testing (October-December 2016), all birds were juveniles (1.5 years). Birds were housed as a group (Colony 3, Appendix A) in a large outdoor aviary (20x10x3m) at the Sub-Department of Animal Behaviour, University of Cambridge. The birds received a maintenance diet of vegetables, eggs, seeds and fruits and water *ad libitum*. All birds took part in Experiment 2.1a. Chinook stopped interacting with the apparatus and the tools after completing this experiment, therefore she was excluded from subsequent experiments. All birds except Chinook were tested in the subsequent Experiments 2.1b, 2.2 and 2.3. All procedures were approved by the University of Cambridge Ethics Review Committee.

Apparatus

All tests were conducted using an object dropping apparatus originally designed by Bird & Emery (2009) and modified for Eurasian jays by Cheke et al. (2011) and Miller et al. (2016). It consisted of a transparent Perspex box (12x11x11 cm) with a baited but out-of-reach, collapsible platform with a vertical tube (11.5 cm) on top (Fig. 2.1). Depending on the experimental condition, either a wide tube (Ø 4.2 cm) or a narrow tube (Ø 1.6

cm) was used. To release the food, birds could drop a tool (e.g. a stone) into the tube, which then caused the internal platform to collapse and food to fall out.

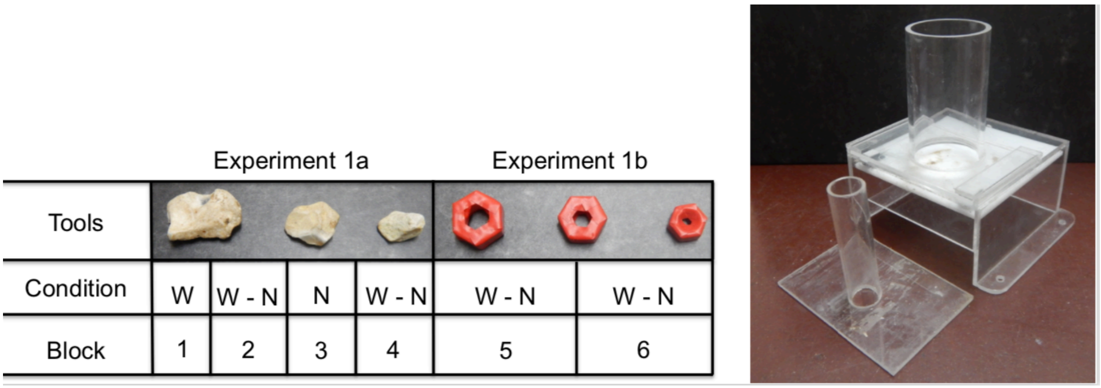

Figure 2.1: Design and Apparatus used in Experiment 1. Left: Scheme showing the tools (stones or novel objects) and conditions (*Wide tube*, W; *Narrow tube*, N) used in each block (20 consecutive trials) in Experiment 1a, and 1b; Right: Picture of the Wide tube apparatus (back) and Narrow tube (front).

General Procedure

Birds were tested in visual isolation from other individuals inside an indoor compartment (2x1x3 m). The experimenter placed the apparatus and the tools into the bird's compartment through an opening in the mesh wall. In all three experiments, the tools were placed on one side of the apparatus, approximately 10 cm away from it. The initial position of the bird was not standardized, so that the bird could be in any location within the compartment at the onset of each trial, i.e. when the stimuli were presented. In experiments involving multiple tools (Experiments 2.1 and 2.2), the tools were equidistant from the bird when the bird was facing the front side of the apparatus (i.e. the side of the apparatus from which the food is released). In Experiments 2.1 and 2.2, the position of the tools in regards to the apparatus (i.e. close, middle, far position) was pseudo-randomized across trials. Live larvae of the mealworms beetle (*Tenebrio molitor*) were used as food rewards. The baiting of the apparatus occurred out of view.

In all experiments the maximum duration of a trial was set to 2 minutes. However, in Experiment 2.3, one additional minute was allowed if the bird was interacting with the tool by the cut-off time (up to 4 minutes in total, i.e. up to two additional minutes were allowed). This procedural detail was set during the very first trial, when it was noticed that the jay being tested required substantially more efforts to achieve the correct manipulation of stick tools.

Typically, birds were given 10 trials per day. However, if a bird did not interact with the tool(s) at all during a trial, testing was interrupted and continued on the next day, with the no-interaction trial being repeated. For example, if a bird completed trials 1-8 and subsequently it stopped interacting with the stimuli on trial 9, then on the day the bird received trial 9 again, and potentially 10 additional trials (i.e. trials 9-18).

Subjects did not have access to their maintenance diet for 1h prior to testing to ensure that they were motivated to eat multiple food rewards during testing. Water was accessible *ad libitum* during testing. All experiments were recorded using a GoPro® Hero 4 video-camera and subsequently analysed.

Refresher Training

All birds had previously been trained to drop hollow metal balls (Ø 2 cm, 4 g) inside the apparatus as part of a previous study (Miller et al., 2016). All birds had also been further exposed to the wide tube apparatus and metal balls in a non-systematic manner. This occurred during January-April 2016, as part of my training in working with the jays. Critically, however, the birds had no prior experience of dropping any of the specific tools used in this study (stones and sticks).

I conducted a short refresher training to ensure that the birds were still familiar with the task and would insert stones into the apparatus. During training, the birds were presented with the wide tube apparatus and a single tool placed approximately 10 cm away from it. In the first 5 trials, they were provided with the metal ball (i.e. the tool with which they had previously been trained) and in the following 5 trials with a medium stone (4.2 ± 0.5 g). All birds successfully solved these 10 trials before testing started.

Data Analysis

Inter-observer reliability was calculated by comparing the behavioural scoring I have recorded with that of a naïve coder (Benjamin Farrar, BF) for the 20% of videos in each experiment. All data were analysed with R.3.5. using the RStudio 1.1.447 wrapper (RStudio Team, 2018). All datasets and R scripts used to conduct the statistical analyses are available on Zenodo (https://doi.org/10.5281/zenodo.3471706)

2.3: EXPERIMENT 2.1: Size Selectivity Test

In the first experiment I explored whether Eurasian jays were capable of tool selectivity when size was the feature determining the functionality of the objects

2.3.1: METHODS

Procedure

The design of this experiment closely followed the 'Stone Size Test' conducted by Bird and Emery (2009) on rooks. I used both the wide and the narrow tube apparatuses in the test. In Experiment 2.1a, stones of three sizes – large (7.8 ± 0.2 g), medium (4.2 ± 0.5 g), small (2.2 ± 0.1 g) – were provided as tools. With the wide tube, stones of all sizes were functional (i.e. all stones could fit inside the tube), whereas with the narrow tube, only the small stone was functional because the two larger stones did not fit inside the tube. The experiment was composed of four blocks (Fig. 2.1). In Block 1 (trials 1-20), jays were presented only with the wide tube apparatus to evaluate their potential preference for a specific tool, namely the small versus the large stone. In Block 2 (trials 21-40), the narrow tube (10 trials in total) and the wide tube (10 trials in total) were presented in a pseudo-randomized order to investigate whether the jays would spontaneously select the small stone when this was the only functional tool (*Narrow tube* condition), and whether they would express the same preference when all stones were functional (*Wide tube* condition). In Block 3 (trials 41-60) only the narrow tube apparatus was used. This block was designed to facilitate jays' learning about the functional features of the small stone. Finally, in Block 4 (trials 61-80) birds received a further test with the narrow and wide tubes that followed the procedure of Block 2. This experiment differed from the 'Stone Selectivity Test' conducted by Bird and Emery (2009) in two respects. Rooks tested in the latter study received a smaller number of trials (i.e. 60 trials), and they experienced only the wide tube apparatus in the first 30 trials and only the narrow tube apparatus in the remaining 30 trials.

After noting that the jays appeared to have switched to using the small stone more often in Block 4 than in Block 2, in Experiment 2.1b I investigated whether jays may have learned to select the small stone based on its functional property, namely its size. To that end, Experiment 2.1b was a transfer task with novel objects, which differed from the stones in irrelevant perceptual properties namely colour, shape and material. In the same way that the stones previously differed in their functional property of size, the novel objects were large (15 g), medium (10.5 g) and small (5 g) bolts upholstered with red tape. Like previously, the novel objects of all sizes were functional with the wide tube but only the small one could fit in the narrow tube. Given that jays had had two blocks of the two apparatuses in a counterbalanced order in Experiment 2.1a, they also received two blocks in Experiment 2.1b (Fig. 2.1): Block 5 (trials 81-100), Block 6 (trials 101-120). In each block, there were 10 trials with the narrow tube in total and 10 trials with the wide tube, the order of which was pseudo-randomized such that the jays did not receive more than three consecutive trials with the wide tube nor narrow tube.

Data Analysis

I scored the size of the tool (small, medium or large) selected on each trial. Ordinal-logit models (package *ordinal*, Haubo and Christensen, 2018) were used to test whether jays adjusted their preference of selection i) according to the condition (*Wide* or *Narrow tube*), and ii) across blocks (e.g. due to learning). In all models, the size of the tool (small, medium or large) selected in each trial was treated as ordinal data and fitted as response variable. Alpha was set to 0.5.

2.3.2: RESULTS AND DISCUSSION

Inter-observer reliability between BF and me was excellent: for the size of selected tools Cohen's kappa was k=0.986. In Block 1, one bird (Stuka) received 15 instead of 20 trials due to an experimental error.

Overall jays selected a similar proportion of the three stones between conditions (Model 1, Tab. 2.1). Hence jays did not adjust the selection of tools according to the diameter of the tube. I further tested whether the proportion of selection of the three stones varied across blocks by comparing jays' performance in Block 1 with each of the three subsequent blocks. The performance in Block 1 represents the spontaneous preference exhibited by the jays when all tools were functional, therefore this block was considered as a meaningful reference to analyse changes of preference through dyadic comparisons among blocks. Model 1 (Tab. 2.1) showed that the proportions of selection of the three stones in Block 1 were comparable to those observed in the two subsequent blocks, but significantly different from the proportions of selection in Block 4. This result is likely to be explained by the variation in preference for the large and the small stones throughout blocks (Figs 2.2 and 2.3). A stronger preference towards the large stone appeared in Block 1 and was retained across Blocks 2 and 3, but it became less pronounced together with an increase in preference for the small stone in Block 4 (Fig. 2.2).

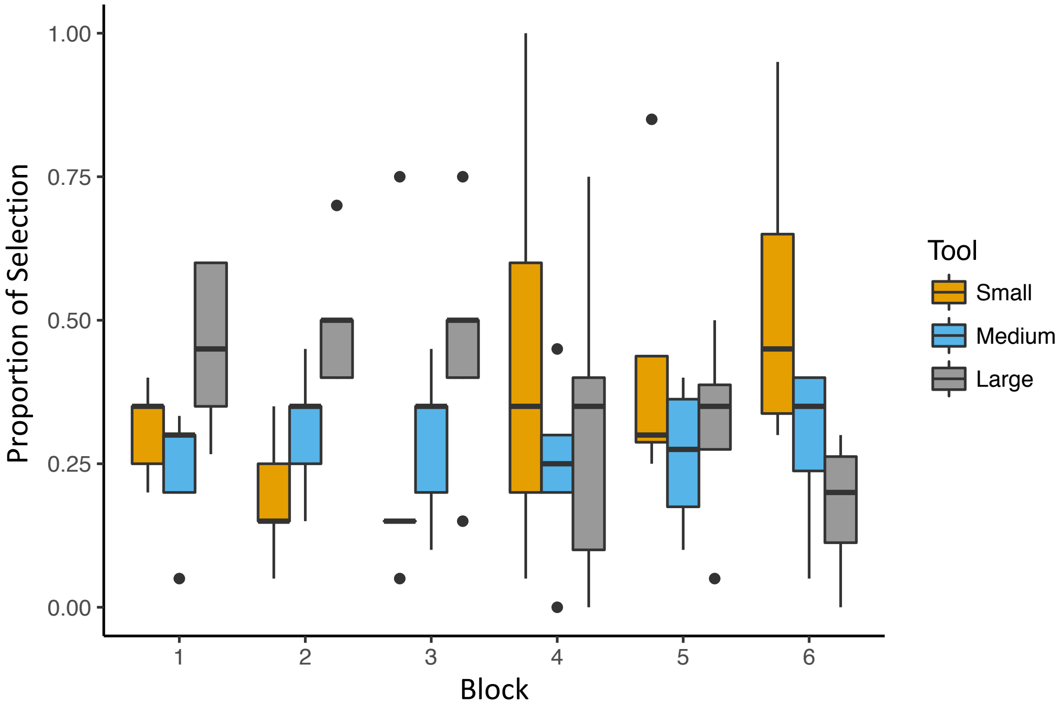

Figure 2.2: Box and Whisker plot showing the proportions of selection of the small, medium and large tool in Experiment 1a (Block 1-4) and Experiment 1b (Block 5,6). In Blocks 2, 4, 5, and 6, the two conditions (*Narrow* and *Wide tube*) are grouped as jays' performance was comparable across conditions (Model 1, Tab. 1).

When presented with novel objects of different sizes for the first time, the jays did not prefer the large tool, rather they chose the three tools in similar proportions (Block 5, Fig. 2.2), thereby seemingly showing a random pattern of selection. To investigate whether this pattern of selection differed from that previously observed toward the stones, I compared the jays' performance in the last block when tools were stones (Experiment 2.1a; Block 4) with the first block when tools were novel objects (Experiment 2.1b: Block 5). One subject (Chinook) was excluded from this analysis because she did not participate in Experiment 2.1b. Model 2 (Tab. 2.1) indicated that the proportions of selection of the three stones (Block 4) and novel objects (Block 5) were not significantly different (Tab. 2.1; Fig. 2.2), thus suggesting that jays showed a similar pattern of behaviours with the stones and the novel objects. In line with previous analyses, Model 2 also indicated that jays' performance was comparable across conditions.

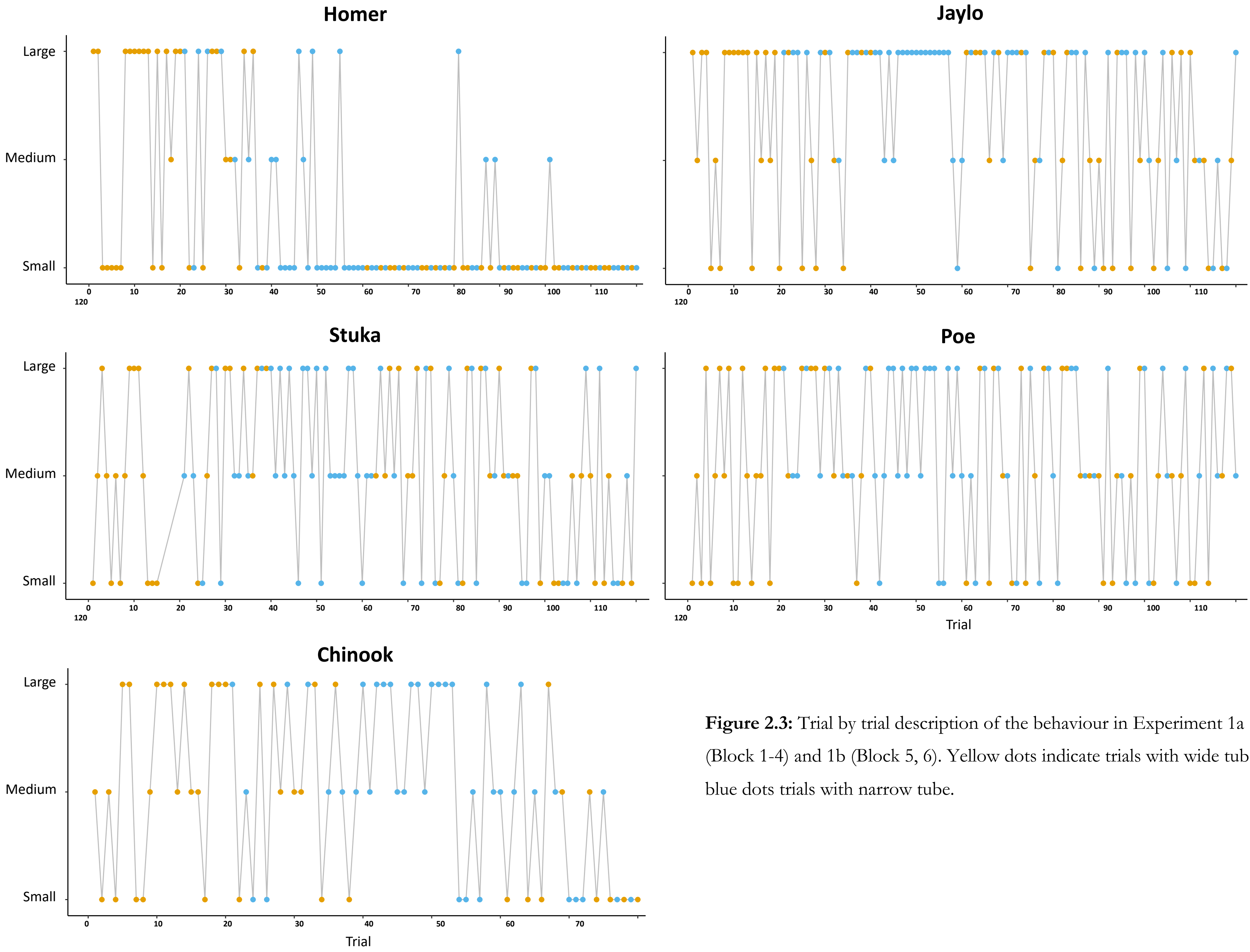

Figure 2.3: Trial by trial description of the behaviour in Experiment 1a (Block 1-4) and 1b (Block 5, 6). Yellow dots indicate trials with wide tube, blue dots trials with narrow tube.

Together, these results are consistent with the possibility that jays transferred their pattern of preference between tools of different appearances. However, I did not test the jays' preference for the three novel objects in a naïve group of birds. Therefore, it cannot be ruled out that jays' performance in Block 5 was not influenced by their experience in Experiment 1a, but rather that it simply resulted from a difference in their spontaneous preference for the novel objects over stones. Specifically, the jays may have had no preference for a novel object of specific size (e.g. large novel object) although they did have an initial preference for the large tool when firstly presented with stones.

Table 2.1: Results from ordinal-logit models examining whether the proportions of selection of the three tools differed: i) according to the condition (*Wide* or *Narrow tube*), and; ii) across blocks of trials. Model 1 focused on Experiment 1a. Model 2 focused on the last block of Experiment 1a and the first block of Experiment 1b. Model 3 focused on Experiment 1b. SE: standard error; z : z value; p: p value.

Model	Variable	Estimate	SE	z	p	
1	Narrow Tube - Wide Tube	-0.13	0.26	-0.50	0.61	
	Block 1 - Block 2	0.24	0.30	0.79	0.43	
	Block 1 - Block 3	-0.03	0.38	-0.09	0.92	
	Block 1 - Block 4	-0.69	0.30	-2.30	0.02	*
2	Narrow Tube - Wide Tube	-0.23	0.29	-0.78	0.44	
	Block 4 (Exp. 1a) - Block 5 (Exp. 1b)	0.18	0.29	-0.60	0.55	
3	Narrow Tube - Wide Tube	-0.43	0.30	-1.45	0.15	
	Block 5 - Block 6	-0.57	0.30	-1.89	0.06	.

Finally, I compared jays' preference of selection of the three novel objects between the two blocks of Experiment 2.1b. Model 3 (Tab. 2.1) revealed that the proportions of selection of the three tools in Block 5 and Block 6 were not significantly different, thus indicating that jays' preferences of selection were stable across blocks. However, the model showed a trend ($p< 0.06$), which could be explained by the concurrent stronger preference for the small tool and decreased preference for the large tool in Block 6 (Fig. 2.2). This pattern first appeared in Block 4, and then it increased – although not significantly – in Block 6 (Fig. 2.2). Supporting previous findings, Model 3 also indicated that jays' performance was again consistent between conditions.

Diagnostic plots were produced for each of the three models. Visual inspection of the plots indicates that all models have a satisfactory fit.

2.4: EXPERIMENT 2.2: Shape Selectivity Test

In this experiment I presented Eurasian jays with a task in which shape – rather than size – represented the property that determined whether a tool was functional.

2.4.1: METHODS

Procedure

The design of this experiment closely followed the 'Stone Orientation Test' used by Bird and Emery (2009) for rooks. In Experiment 2.2, jays were provided with two shapes of stone tools: long stones (approximately 2.4x1.0 cm) and round stones (approximately 1.8x1.9 cm). Birds received a total of 20 trials, 10 of which were with the narrow tube and 10 of which were with the wide tube. The order in which birds were presented with the narrow and wide tubes was pseudo-randomized such that the jays did not receive more than three consecutive trials with the same tube. To successfully solve the task in the *Narrow tube* condition, birds had to select the long stone and orient it vertically to insert it into the tube. In the *Wide tube* condition, both stones were functional and no specific rotation of the tool was required. This experiment and the equivalent test previously conducted on rooks (Bird and Emery, 2009) differed in the number of trials (40 trials in rooks) and in the fact that in the rook study the two apparatuses were not counterbalanced within sessions of trials: rooks first received 20 trials with the wide tube apparatus, and subsequently 20 trials with the narrow tube apparatus).

Data Analysis

I scored the tool (long or round stone) selected and what kind of manipulation of the long stone was performed on each trial. Specifically, three kinds of manipulation could be achieved. The long stone could: i) be oriented vertically prior of the first insertion attempt (*Immediate Rotation*); ii) be oriented vertically after one or more failed insertion attempts (*Eventual Rotation*), or; iii) not be oriented vertically (*No Rotation*). The scoring of these behaviours had been planned before the experiment was conducted, based on the results previously reported in rooks on this test (Bird and Emery, 2009).

Binomial General Linear Models (package *stats*, R Core Team and contributors worldwide, 2018) were fitted to test whether the kind of tool selected and the manipulation performed varied i) according to the condition and, ii) across blocks (e.g. due to learning). Alpha was set to 0.5.

2.4.2: RESULTS AND DISCUSSION

Inter-observer reliability between BF and me was excellent for the shape of selected tools (Cohen's kappa, *k*=1) and the kind of rotation of the tool (Cohen's kappa, *k*=1).

When presented with a choice of two stones of different shapes, jays showed a pronounced preference for the long stone in both conditions (*Narrow tube*: 77.5 ±7.5% trials; *Wide tube*: 77.5 ±4.8% trials; Mean ± SE; Fig. 2.4). The GLM analysis indicated that jays' preference for the long stone was stable across conditions and blocks (Model 4, Tab. 2.2).

Table 2.2: Results from GLMs examining data of Experiment 2. Model 4 tested whether the proportions of selection of the tools (long and round stones) differed: i) according to the condition (*Wide* or *Narrow tube*), and; ii) across blocks of trials. Model 5 tested whether the proportions in which the long stone was oriented vertically (i.e. *Immediate Rotation*, *Eventual Rotation*) or it was not oriented vertically (*No Rotation*) differed: i) according to the condition (*Wide* or *Narrow tube*), and; ii) across blocks of trials.

Model	Variable	Estimate	SE	z	p	
4	Intercept	-1.38	0.47	-2.94	0.003	**
	Narrow Tube - Wide Tube	-0.01	0.54	-0.03	0.98	
	Block 1 - Block 2	0.29	0.54	0.53	0.60	
5	Intercept	1.50	0.53	2.81	0.005	**
	Narrow Tube - Wide Tube	-2.16	0.59	-3.63	0.0003	***
	Block 1 - Block 2	0.16	0.59	-0.27	0.79	

In line with previous findings in rooks (Bird and Emery, 2009), the jays performed three kinds of manipulation when the Long stone was selected. The tool was oriented vertically (Fig. 2.5) either prior to the first insertion attempt (*Immediate Rotation*) or after one or more unsuccessful attempts (*Eventual Rotation*). Alternatively, the tool was oriented horizontally with respect to the tube (*No Rotation*, Fig. 2.5).

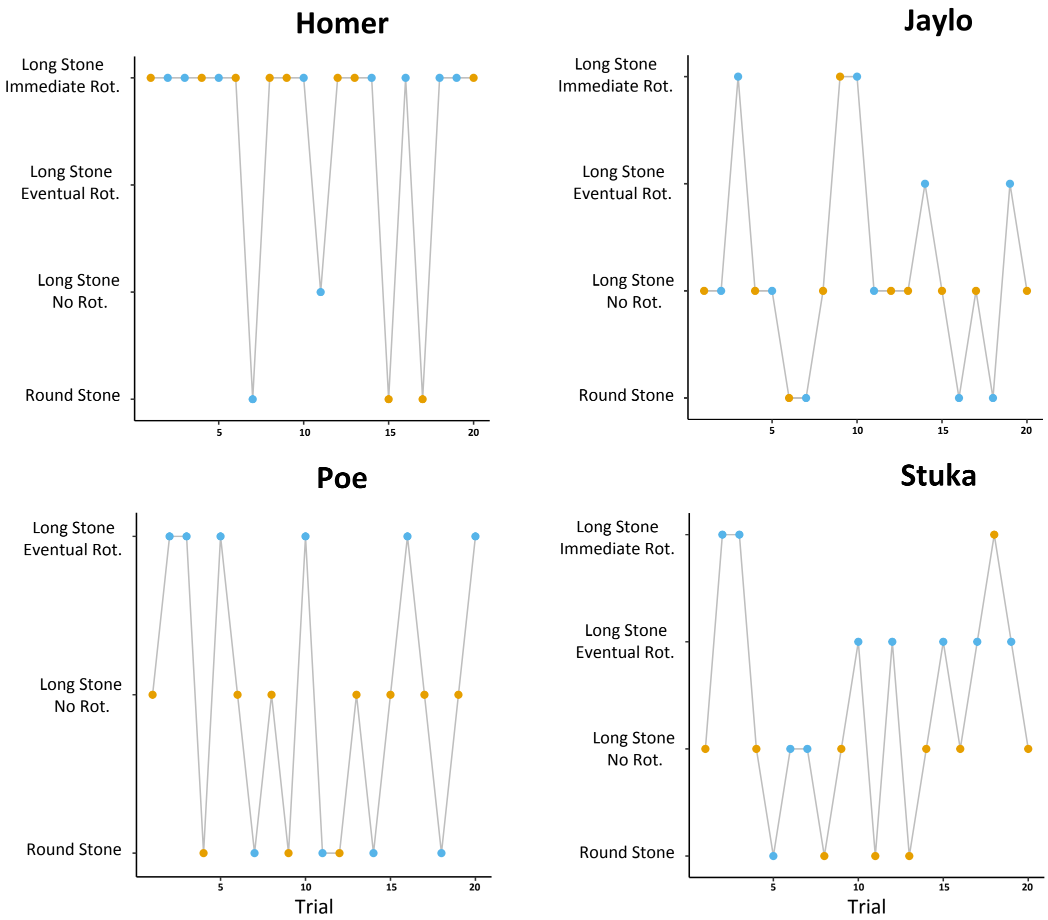

Figure 2.4: Trial by trial description of the behaviour in Experiment 2. Yellow dots indicate trials with the wide tube, blue dots indicate trials with the narrow tube. Note that two individuals performed only two of the three possible kinds of manipulation of the long stone: Homer never performed *Eventual Rotation*, whereas Poe never performed *Immediate Rotation*.

To investigate whether the manipulation of the long stone differed between conditions I fitted a GLM with a binary outcome variable (*No Rotation*-Rotation). The manipulation of the long stone differed between the conditions (Model 5, Tab. 2.2) with higher frequencies of rotation performed with the narrow tube (79.1 ±10.1% trials; Mean ± SE). However, the correct orientation of the long stone in the *Narrow tube* condition was often achieved *after* one or more incorrect attempts of insertion (*Eventual Rotation*: 55.3 ± 21.1% of trials with the narrow tube in which the long stone was rotated; Fig. 2.4). Therefore, this finding cannot be taken as evidence that jays had a solid understanding of the affordance of the task, because in this case they would have correctly oriented the stone before the first insertion attempt (*Immediate Rotation*). Model 5 (Tab. 2.2) also indicated that the manipulation of the long stone was stable across blocks.

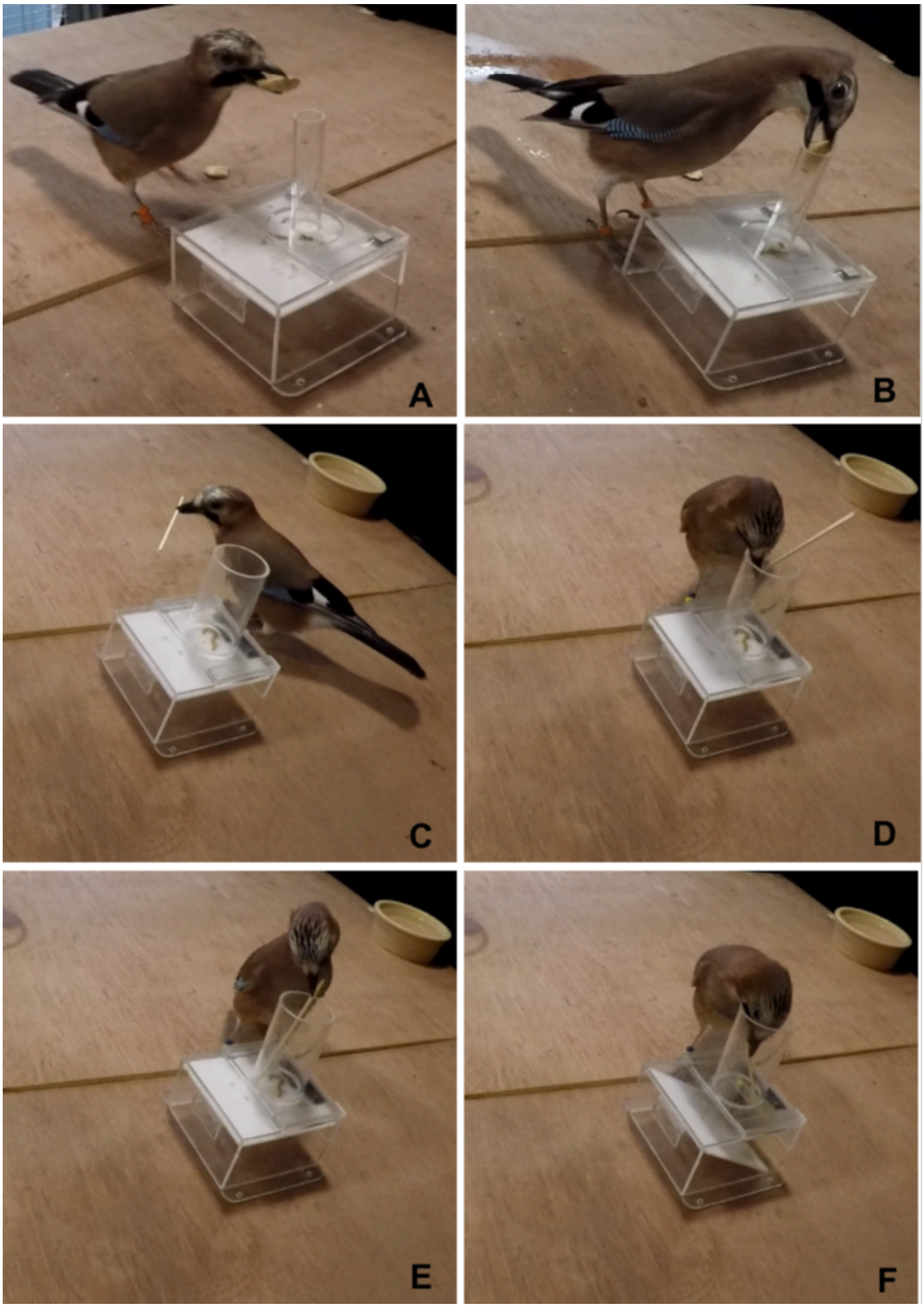

Figure 2.5. Eurasian jay being tested in Experiment 2 and Experiment 3. A-B) Different kinds of manipulation of the Long stone: *No Rotation* (A), Rotation (B); C-F) Sequence of actions describing the *Push* technique: the stick is picked up near one end (C), steered inside the tube (D) and pushed downward (E) causing the collapse of the internal platform of the apparatus (F).

2.5: EXPERIMENT 2.3: Stick Tool Test

In the third experiment I explored whether Eurasian jays can use sticks as tool to solve a task with the same apparatus.

2.5.1: METHODS

Procedure

The design of this experiment closely matched the 'Stick Use Test' conducted by Bird and Emery (2009). In Experiment 2.3, jays were provided with one of two types of sticks as a tool: a twig (11 cm long, 3.0 g) or a barbecue stick (11 cm long, 0.4 g). When provided with the twig, jays could solve the task by dropping it, just like they previously did with stones (*No Push* technique). Due to its lighter weight, the barbecue stick required jays to hold it in their beak and push it downwards to collapse the baited platform (*Push* technique).

A total of 10 trials with the wide tube were conducted. On each trial, jays were only provided with one type of tool (the barbecue stick or the twig), the order of which was pseudo-randomized such that jays did not receive the same tool on more than two consecutive trials.

In contrast to this experiment, rooks tested by Bird and Emery (2009) received more trials (20 trials) and they were presented consistently with the heavy stick in the first 10 trials, and then the light sticks in the final 10 trials.

Data Analysis

I scored: i) whether a trial was successful, ii) the technique utilized to solve the task with stick tools (i.e. *Push* technique, *No Push* technique), and iii) the number of insertion attempts until successfully inserting the tool into the apparatus. The scoring of successful trials and the tool use technique had been planned before the experiment was conducted, based on the results previously reported in rooks on this test (Bird and Emery, 2009). I decided to score the number of insertion attempts during the testing phase as it became clear that this variable was very informative of inter-individual differences in performances. The data were analysed descriptively.

2.5.1: RESULTS AND DISCUSSION

Inter-observer reliability was again excellent: BF and I achieved 100% of agreement in scoring successful trials and insertion techniques.

All subjects solved the task by using a stick as a tool (Tab. 2.3). However, the insertion rate was extremely variable: Homer 9/10 trials, Jaylo 8/10 trials, Poe 2/10 trials, Stuka 1/10 trials. Similarly, the number of insertion attempts was also quite variable among subjects (Tab. 2.3). The success rate matched the insertion rate for all subjects except for Jaylo, who did not collapse the platform in the three trials in which the tool was inserted into the apparatus.

Table 2.3: Trial by trial description of the behaviour in Experiment 3. In successful trials (blue cells), the technique that was used is reported. Blank cells correspond to unsuccessful trials.

	Homer				Jaylo			
Trial	**Stick Kind**	**Inserted**	**N°Attempts**	**Technique**	**Stick Kind**	**Inserted**	**N°Attempts**	**Technique**
1	BBQ Stick	Y	2	Push	BBQ Stick	N	14	
2	Twig	N	5		Twig	Y	12	Push
3	BBQ Stick	Y	2	Push	BBQ Stick	N	12	
4	BBQ Stick	Y	2	Push	BBQ Stick	Y	7	
5	Twig	Y	2	No Push	Twig	Y	7	Push
6	Twig	Y	13	Push	Twig	Y	3	Push
7	BBQ Stick	Y	1	Push	BBQ Stick	Y	9	
8	Twig	Y	3	Push	Twig	Y	5	Push
9	Twig	Y	1	No Push	BBQ Stick	Y	8	
10	BBQ Stick	Y	3	Push	Twig	Y	1	Push
	Poe				**Stuka**			
Trial	**Stick Kind**	**Inserted**	**N°Attempts**	**Technique**	**Stick Kind**	**Inserted**	**N°Attempts**	**Technique**
1	BBQ Stick	N	16		Twig	N	1	
2	Twig	Y	11	No Push	Twig	Y	5	Push
3	BBQ Stick	N	16		BBQ Stick	N	4	
4	BBQ Stick	Y	9	Push	Twig	N	4	
5	Twig	N	15		Twig	N	2	
6	Twig	N	0		BBQ Stick	N	0	
7	BBQ Stick	N	2		BBQ Stick	N	0	
8	Twig	N	0		Twig	N	0	
9	BBQ Stick	N	0		BBQ Stick	N	0	
10	Twig	N	0		BBQ Stick	N	0	

In most of the successful trials (77%), jays collapsed the platform of the apparatus by actively pushing downward on the stick (*Push* technique). The technique was adopted not only with light barbecue sticks but also with twigs. In 23% of successful trials, the insertion of the twig into the apparatus was sufficient to collapse the platform in the absence of active pushing (*No Push* Technique). The reason for the active pushing with the heavy stick can likely be explained by the insertion technique used by the birds. Instead of dropping the stick as they did with stones, birds typically held the stick near one end and appeared to carefully steer it inside the tube (Fig. 2.5). As a result of these seemingly gentle movements, the heavy stick likely did not always hit the platform with enough force to collapse it. All birds used the *Push* technique at least once. Two subjects (Homer and Poe) solved the task by using both techniques.

2.6: GENERAL DISCUSSION

In this chapter I investigated the tool use abilities of Eurasian jays by exploring whether this corvid species can select functional tools on the basis of their physical properties, namely size and shape, and solve a familiar task by using novel tools, in this case sticks. Jays showed only limited tool selectivity, i.e. they did not spontaneously adjust their choice according to the functionality of the tools, but were capable of using sticks as tools.

In the size selectivity test (Experiment 2.1), jays initially exhibited a spontaneous preference for the large stone regardless of whether this tool was functional. Thus, jays seem to have failed to encode the relevant feature of objects and to adjust their selection of tool according to the features of the apparatus. However, jays' performance also suggests that they may be capable of altering their selection of tools through learning: across trials jays reduced their initial preference in favour of the only tool that was functional in both conditions, namely the small stone. Subsequently, when presented with novel objects (Experiment 2.1b), jays expressed a pattern of selection that was comparable to those observed toward stones in the final block of the previous test (Experiment 2.1a). This result is consistent with the possibility that jays transferred their preference of which tool to use based on size despite other perceptual differences between the objects (perhaps through a process of generalization, cf. Shettleworth, 2010).

In the shape selectivity test (Experiment 2.2) jays exhibited a pronounced preference for the functional tool (long stone) in both conditions, but they tended to perform the correct manipulation of the tool only when needed (*Narrow tube* condition). However, jays often achieved the correct manipulation of the tool after one or more failed attempts of insertion (*Eventual Rotation*) rather than before the first insertion attempt (*Immediate Rotation*). Therefore, it is likely that jays correctly oriented the tools through trial-and-error, in the lack of a full understanding of the objects' properties and functionality.

In the stick tool test (Experiment 2.3), all birds were capable of using a novel tool and of acquiring food rewards from a familiar apparatus through a novel strategy (i.e. *Push* technique). These results also represent the first demonstration that Eurasian jays can use sticks as tools.

The overall pattern of our results supports previous reports of learning forming the basis of Eurasian jay tool use (Cheke et al. 2011). The relatively fast learning of a preference for the functional tools in the latter study may have been facilitates by the fact that birds had already experienced the functional sinking objects as tools, before the experiment (Cheke et al. 2011) and that the functional and non-functional tools differed not only in the relevant characteristic (density) but also in others features (material and colour). Furthermore, in line with Cheke et al. (2011), I found important individual differences in tool use skills in Eurasian jays. One bird, Homer, rapidly developed a clear preference for the functional small tool in Experiment 1 (Fig. 2.3) compared with the other jays that were tested; Homer more frequently oriented the tool correctly *before* the first insertion attempt (*Immediate Rotation*) in Experiment 2 (Fig. 2.4) and solved more trials (9/10) and by using both techniques in Experiment 3 (Tab. 2.3). A possible explanation for the performance of this individual may be linked to his experimental history. Homer was used as the demonstrator in a previous tool use study (Miller et al., 2016) and thus has received a more extensive exposure to the object-dropping apparatus than the other individuals we tested.

Given that neither Eurasian jays nor rooks habitually use tools in the wild, it is interesting to compare the performance of the jays in this study with that of the rooks tested by Bird and Emery (2009). Importantly, however, one must exhibit caution in doing so given that these were two separate experiments, but tentative comparisons might yield fruit for further work in which the two groups of birds could be directly compared. When tested in a similar size selectivity test, rooks immediately switched their preference from the large stone to the small stone when the latter was the only functional tool (Bird and Emery, 2009). In the shape selectivity test, rooks, like jays in this study, expressed a pronounced preference for the long stone regardless of the condition, and higher frequencies of rotation in presence of the narrow tube (Bird and Emery, 2009). Crucially however, rooks often performed *Immediate Rotation* rather than *Eventual Rotation* in the *Narrow tube* condition. Taken together, the performances of these species may indicate that Eurasian jays may have more limited tool selectivity abilities than rooks (Bird and Emery, 2009). However, this possibility should be considered with caution given the methodological and ontogenetic differences between our experiments and those conducted by Bird and Emery (2009). Specifically, in Bird and Emery's (2009) selectivity tests, rooks were systematically presented with the wide tube apparatus in the first half of trials, and subsequently with the narrow tube apparatus in the remaining trials. In contrast, the jays tested in this study did not experience such a clear sequence of exposure to the two apparatuses, as the presentation of the two apparatuses most often co-occurred within the same block of trials. Although apparently minor, it cannot be excluded that this methodological difference may have influenced the performances of the two species. Another potentially relevant difference between the studies is that jays tested in this study were juveniles (1.5 years old at test date) whereas the rooks tested by Bird and Emery (2009) were adults at the time of testing.

In regard to the stick tool test jays' performance appears to be similar to that reported in rooks (Bird and Emery, 2009). Both species appear to exhibit good levels of flexibility in using novel tools to solve a familiar task. Supporting previous findings in rooks (Bird and Emery, 2009), jays' use of sticks as tools also indicate that New Caledonian crow-like adaptations in beak morphology and vision (Martinho et al., 2014; Matsui et al., 2016; Troscianko et al., 2012) are not essential to achieve basic manipulations of stick tools.

Ultimately, to directly assess the question of whether the sophisticated physical cognition reported in the *Corvus* genus is shared with more distantly related species of corvids, future work will have to encompass large-scale comparative studies, where different species can be directly compared using the same or equivalent methodology.

In summary, after being trained to use stones as tools, the Eurasian jays were able to generalise to using sticks and to adopt a novel technique on the same apparatus, i.e. collapsing the internal platform by actively pushing a tool against it. What appears to be in contrast to the previously reported results for rooks is that the Eurasian jays failed to immediately adjust their selection of tools according to their functionality. However, the jays' performance indicates that these birds were capable of learning to optimise their behaviour, as they progressively developed a preference for the smaller size tool, which was the only tool that was functional in both conditions, and performed the required manipulation of the functional long-shaped tool.

As introduced in Chapter 1, physical problem solving is considered to be one of the cornerstones of cognitive sophistication. In Chapter 3, I therefore continue my investigation into the cognition of the Eurasian jay by focusing on a second cognitive pillar, namely prospection.

CHAPTER 3:

Testing two competing hypotheses for Eurasian jays' caching for the future: planning versus compensatory caching

Abstract

On par with physical problem solving – which I investigated in Chapter 2 – prospection ability is thought to be a key cognitive pillar. Previous research reported that jays could provision for future events: they cached more food in a location where no food was going to be available at a later point and cached more of a specific food in a location where this food was not going to be available. In this chapter, I consider two competing hypotheses that could explain this caching behaviour. The birds either learn to cache more in places where food was less frequently available in the past (Compensatory Caching Hypothesis) or they recall what-when-where features of past events to predict future availability of food (Future Planning Hypothesis). I tested Eurasian jays in two experiments using a protocol that aims at disambiguating the two hypotheses: the expected caching pattern under the Compensatory Caching Hypothesis differs from the one under the Future Planning Hypothesis. Consistently across the two experiments, data did not support either hypothesis. Future research is needed to gain more insights into the cognitive underpinnings of corvids' caching for the future.

3.1: INTRODUCTION

As discussed in Chapter 1, corvids are also one of the prominent animal models for the study of prospection (Clayton and Emery, 2015; Emery, 2004; Emery and Clayton, 2004; Seed et al., 2009a). Over the last two decades, an increasing number of studies in corvids and other animals, primarily apes, have challenged the view that future planning abilities evolved only once, in humans (primates: Mulcahy and Call, 2006; Naqshbandi and Roberts, 2006; Osvath, 2009; Osvath and Karvonen, 2012; Osvath and Osvath, 2008; corvids: Cheke and Clayton, 2012; Correia et al., 2007; Kabadayi and Osvath, 2017; Raby et al., 2007; rodents: Pfeiffer and Foster, 2013). In particular, California scrub-jays and Eurasian jays were found to adapt their caching behaviour according to future needs. Experiments showed that these jays tend to cache more in locations where food will be absent in following trials, or cache preferentially a specific type of food (relatively to another type of food) in locations where that food will not be available in following trials (Cheke and Clayton, 2012; Correia et al., 2007; de Kort et al., 2007; Raby et al., 2007).

The jays' performance in these studies is in line with the Future Planning Hypothesis: namely that at the time of caching, jays may have recalled the 'what-when-where' features of past events (e.g. the availability of a specific food in a given location at a given time) and cached food that will maximize the future outcome. Remarkably, jays' may be able to do so even when their motivational state at the time of caching differs from their motivational state at recovery, thus suggesting that their caching decision is not based on their current motivation. One manner in which an individual's current motivation can be manipulated is through sating an individual on a specific food. This procedure subsequently reduces the individual's motivation for eating that specific food (but not different kinds of food), a phenomenon known as specific satiety (Balleine and Dickinson, 1998; Dickinson and Balleine, 1994). Building on this phenomenon, Cheke and Clayton (2012) and Correia et al. (2007) found that jays cached preferentially a type of food that will not be available in the future even when they had a low desire toward that food at the time of caching, because they have been sated on that food before being allowed to cache. Additional support for the Future Planning Hypothesis comes from experiments demonstrating that jays are capable of episodic-like memory (Clayton and Dickinson, 1998), i.e. they can retrieve information about *what* happened in a specific event, *where* it took place, and *when* it occurred (Clayton et al., 2001). This is because: i) the Future Planning Hypothesis hinges on the ability of recalling 'what-where-when' features of past events; ii) episodic-like memory and future planning are thought to be based on the same cognitive machinery (Clayton et al., 2003; Suddendorf and Corballis, 2007) and show the same developmental trajectory in young children (Clayton, 2015).

However, it has been argued that jays' performance in these caching experiments cannot be taken as evidence of future planning abilities because the experimental designs do not exclude alternative interpretations of the results. Two predominant alternative explanations that have been raised are the Mnemonic Association Hypothesis and the Compensatory Caching Hypothesis (see below). Importantly, each of these hypotheses cannot provide an alternative interpretation for all published caching experiments, but only to a specific subset of the studies. Yet the Mnemonic Association Hypothesis and the Compensatory Caching Hypothesis are not necessarily mutually exclusive – rather they may describe two parallel cognitive processes – so that they can, together, explain the currently available results.

The Mnemonic Association Hypothesis (Dickinson, 2011; see also Cheke and Clayton, 2012;) suggests that jays' strategic caching behaviour may be the result of long-delay learning (Lett, 1975): at the time of the outcome (e.g. recovery), jays may have recalled their previous actions, and thus created a positive association with the specific action that had resulted in a more beneficial outcome (e.g. the action of caching a specific type of food). This mechanism hinges on episodic-like memory because the retrieval of the 'what-when-where' features of a past episode is essential to develop a positive association between an outcome experienced in the present and the action that was performed in the past and that led to that outcome. Thus, although both the Mnemonic Association Hypothesis and the Future Planning Hypothesis postulate 'what-where-when' memory, the former explains the jays' strategic caching as the result of a learning process. In the studies conducted by Correia et al., (2007), de Kort et al., (2007), and Cheke and Clayton (2012), jays may have – during the second and third caching session – reiterated the actions which led to the more beneficial outcome in the first recovery session, thereby solving the tasks without pre-experiencing future scenarios.

Crucially however, while the Future Planning Hypothesis can explain the data from all experiments, the Mnemonic Association Hypothesis cannot provide an explanation for the results of Raby et al. (2007). Here, on six consecutive days, Californian scrub-jays had access to either compartment A or B, with the availability of food during the first two hours being dependent on the compartment (Fig. 3.1). When in the evening of the sixth day the jays were allowed to cache for the first time, they cached more food in the compartment where no food was available on the previous mornings (Raby et al., 2007). In a follow-up experiment, each of the two compartments was associated with a specific type of food (e.g. food X available in compartment A, food Y available in compartment B). Here, in the test trial, jays cached proportionately more items of each food in the compartment in which they had experienced the alternate food being available (Raby et al., 2007). These results are consistent with the Future Planning Hypothesis: jays may have adjusted their caching strategy according to their expectations of the specific future event, thereby ensuring that on the hypothetical following day, i) food will be available in the compartment where they experienced hunger on the previous days (in Experiment 1), and; ii) both types of foods will be present in the two compartments (in Experiment 2). In contrast, these results cannot be explained by the Mnemonic Association Hypothesis. Because jays were given a single caching trial (i.e. at test), their caching pattern could not have resulted from long-delay learning, i.e. jays could not have adjusted their caching behaviour according to the outcome of a previous caching event. (Dickinson, 2011). Nevertheless, it has been argued that jays' performance in this study may not entail any kind of prospection ability: jay may 'have a propensity to cache a particular food type in a given location that differs from the foods that have been previously associated with that location, a strategy that would provide more uniform distribution of resources' (Shettleworth personal communication, as cited in Dickinson, 2011, page 90; see also Premack, 2007; Suddendorf and Corballis, 2008). Support to this idea is, to some extent, provided by field observations: wild American crows (*Corvus brachyrhynchos*) foraging at walnut trees were never observed caching nuts in proximity of the fruiting trees but carried the items up to 2km away before caching them (Cristol, 2001). This argument, henceforth referred to as the Compensatory Caching Hypothesis, appears to bear high ecological relevance also in the case in which two different types of food are available. As pointed out by Shettleworth (2010) 'For an animal that caches different types of items (and […] can remember what it cached where), a strategy of distributing items of each type as widely as possible would help to defeat predators that might raid just one of those types' (page 393). Since caching behaviour is considered to have played a key role in the evolution of corvid cognition (de Kort and Clayton, 2006; Grodzinski and Clayton, 2010), it appears plausible that, to protect their caches, these birds may have developed predispositions such as those assumed by the Compensatory Caching Hypothesis.

To reach firmer conclusions on whether caching behaviour in corvids entails prospection abilities, it is essential to test the Future Planning Hypothesis against each of the two predominant alternative interpretations. As the Mnemonic Association Hypothesis and the Compensatory Caching Hypothesis may describe two complementary processes, these hypotheses should first be investigated independently. In this chapter I focus on the Complementary Caching Hypothesis. Firstly, I describe a cognitive mechanism that may underpin jays' propensity to distribute caches such that across different locations, resources are uniformly distributed. Secondly, I report a paradigm that allows to test the Complementary Caching Hypothesis against the Future Planning Hypothesis in jays.

Following Brea and Gerstner (2019), jays may evaluate the suitability of a given location as caching site for a specific type of food by attributing location-specific 'weights' according to the perceived availability of that food in that location. For instance, if a jay is given the possibility to access three potential caching locations (A, B, C), in which no food was experienced, then the bird may attribute equal weights to each location (wA, wB, wC), and therefore, if allowed to cache, distribute caches in comparable quantities across the locations. However, if the jay subsequently experiences a given food as being available in a given location (e.g. at location A), then the location-specific weights may be updated accordingly, i.e. wA is reduced in comparison to wB and wC. As a result, when allowed to cache, the jay may concentrate its caches in the two locations associated with higher weights for this food (e.g. locations B and C), thus achieving a more uniform distribution of the resources. This idea is similar to that proposed by Hampton and Sherry (1994) as a possible mechanism employed by black-capped chickadees for re-using caching locations according to the probability of recovering previously hidden items.

Building on Raby et al. (2007)'s study, a paradigm was developed to differentiate between the Compensatory Caching and the Future Planning Hypotheses (Fig 3.1). Eurasian jays first received an experience phase over nine consecutive days. On each day, jays had access to one of three compartments, in which a specific food (either food X or Y) was available. Crucially, the location and the type of food available on each day changed respectively on a 3-days cycle and on a 2-day cycle (Fig. 3.1). Thus, jays experienced the three compartments as being differentially associated with each specific food. Subsequently a single test trial was conducted in which jays could freely cache both foods in all three locations.

Raby et al. (2007)

	Experience Phase						**Test**
Days	1	2	3	4	5	6	(evening Day 6)
Compartment	A	B	A	B	A	B	
Condition	X	Y	X	Y	X	Y	

Chapter 3

	Experience Phase									**Test**
Days	1	2	3	4	5	6	7	8	9	(evening Day 9)
Compartment	A	B	C	A	B	C	A	B	C	
Condition	X	Y	X	Y	X	Y	X	Y	X	

Figure 3.1: Experimental protocols**.** On training days, the birds could access one of the compartments (A, B or C) under condition X or Y, where X could mean that no food is provided or only food of a certain type, and Y could mean that food is provided or only food of another type. In the protocol of Raby et al. (2007), each compartment is always experienced under the same condition. In the experiment reported here, each compartment is experienced under both conditions.

This design ensures that the two competing hypotheses have opposite predictions. According to the Compensatory Caching Hypothesis, birds are expected to cache a similar number of items in the three test compartments, but they should allocate the two types of food with different proportions across the three compartments: specifically, they should exhibit a preference for caching in each compartment the food that was – during the experience phase – less frequently experienced in that specific compartment. In contrast, the Future Planning Hypothesis predicts that birds should exhibit a preference for caching according to which location they would have access to on the future days (i.e. hypothetical additional trials equivalent to the past experience trials) and according to what food would be available there. Two possible, complementary, predictions would support the Future Planning Hypothesis: jays could plan only for the nearest future event (hypothetical trial 10) or they could take into account all future events that they can currently provision for (hypothetical trials 10, 11, and 12). According to the former (Prediction 1), jays should cache more items of the food that they expect will not be available, and only in the compartment that they expect will be accessible on the hypothetical trial 10. According to the latter (Prediction 2), jays should distribute their caches across all three compartments but cache more food in the specific compartment where they expect that particular food will not to be provided the next time that they would have access to that particular compartment (hypothetical trials 10, 11, and 12). Importantly, the two predictions differ only in whether caching is expected in the two compartments that correspond to the hypothetical days 11 and 12.

3.2: EXPERIMENT 3.1

3.2.1: METHODS

Subjects

Nine Eurasian jays of both sexes (four males, five females; all born in 2007) participated in the study: Caracas, Lima, Lisbon, Dublin, Rome, Jerusalem, Wellington, Washington and Quito. Birds were housed as a group (Colony 1, Appendix A) in a large outdoor aviary (20x10x3 m) at the Sub-Department of Animal Behaviour, University of Cambridge, Madingley. The sample size included all birds that were available when the study was conducted. Two other colonies (i.e. Colony 2 and 3) that are housed at the same site were not tested because these birds were being used in other studies at that time; thereby it was not possible to install the set-up required for the experiments reported here in their indoor testing compartments. Outside of testing the birds had *ad libitum* access to their maintenance diet, which consisted of vegetables, eggs, seed and fruits. Water was available at all times. All procedures were approved by the University of Cambridge Ethics Review Committee. The study was conducted in October-December 2017.

Experimental Set-up

The experimental set-up comprised three indoor test compartments (labelled as A, B, C) that were accessible from an equidistant middle compartment (Fig. 3.2). All four compartments (1x1x2 m) were delimited by mesh walls and contained a suspended wooden platform (1x1 m). Birds could access the set-up from a trap-window connecting the outside aviary with the middle compartment, and from there they could reach each test compartment through an opening in the mesh wall. The openings of the three test compartments could be opened and closed. Whilst standing outside the compartments, the experiment could lower and raise transparent Perspex windows in the openings by using ropes.

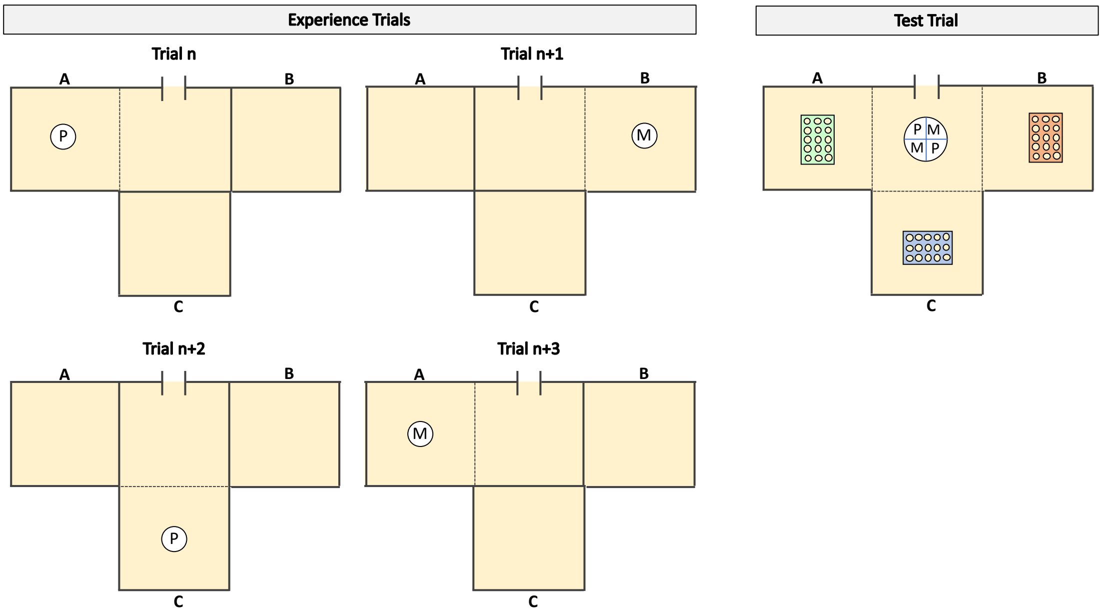

Figure 3.2: Top view of the experimental set-up of Experiment 3.1. Birds could access the three test compartments (A, B, C) from a middle compartment. On each experience trial (Left), the bird had access only to one test compartment (e.g. A in Trial n; B in Trial n+1), and one type of food in powdered form (e.g. Peanuts (P) in Trial n; Macadamia nuts (M) in Trial n+1). The compartment that was accessible and food available rotated respectively on a 3-days cycle and on a 2-days cycle. On the test trial (Right), a bowl containing items of both types of food was placed in the middle compartment and caching trays were placed in all test compartment. Birds could freely move and cache in all compartments.

Pre-Test

The test procedure required that jays in principle eat powdered food in sufficient quantity to develop specific satiety. Note that it was essential to use food in powdered form so that jays could not cache inside the experimental set-up during the experience phase. To ensure that jays would meet these requirements, a Pre-test was conducted.

Each bird received two pre-test trials in total. The birds' maintenance diet was removed from the aviary approximately 1.5 h prior to the start of each trial. Birds were tested in visual isolation from the rest of the group, namely in an indoor compartment that was not part of the experimental set-up. Trials were conducted on different days and involved a pre-feeding phase followed by a test phase. On each trial, birds were first provided with a bowl containing 50.0 g of powdered food (either peanuts or Macadamia nuts) and given the opportunity to eat for 15 minutes. Following this pre-feeding phase, the powdered food bowl was removed and birds received two bowls, one containing 50 whole peanuts, and one containing 50 Macadamia nut halves. Birds could freely eat and manipulate (and thus also cache in the compartment) both types of food during the test phase (15 minutes). At the end of each trial, I recorded: i) the amount of powdered food taken out of the bowl during the pre-feeding phase, and; ii) the number of items of both food that were taken from the bowls in the testing phase. Across the two trials, all birds experienced both types of food in powdered form in the pre-feeding phase. The order in which the two types of foods were presented was counterbalanced across birds. To pass the pre-test, birds were required to i) take at least one peanut and one Macadamia nut from the respective bowls across the two trials, and ii) exhibit an eating pattern that was numerically in line with specific satiety, i.e. to show a relative preference for the non-pre-fed food when both trials were considered. For instance, a jay should have taken a smaller number of peanuts after being pre-fed peanuts than after being pre-fed Macadamia nuts. If a bird did not meet the criteria on the first pair of trials, it was re-tested a second time.

Familiarization

After the Pre-test, the birds were familiarized with the experimental set-up in one trial. Birds were individually given access to the middle compartment and allowed to explore all three testing compartments. At this stage all compartments' windows were kept open. Three items of a high value food not used as a test food in the test (wax moth larvae, *Galleria mellonella*) were placed in each test compartment to favour the exploration of the areas. The bird inside the set-up was monitored remotely through a cctv camera system. The duration of the familiarisation was not the same for all birds: a bird was released back into the aviary through the trap-window in the middle compartment after it has eaten in all compartments. However, if a bird showed no motivation for the food or otherwise looked as if they were not comfortable in the set-up (e.g. flying frantically across compartments), the trial was concluded and the bird released into the outdoor aviary. No standardised duration was set for the trials. The decision regarding how long a bird was inside the set-up was made by the experimenter on a case-by-case basis. To successfully complete the Familiarization, birds were required to eat at least one food item in each test compartment. In case a bird did not reach this criterion, the

Familiarization trial was repeated up to two times (i.e. birds could receive three Familiarization trials in total).

Test

The experiment consisted of an experience phase (nine trials), followed by one test trial. In the experience phase birds received one trial per day on nine consecutive days. The trials were conducted in the morning after the birds' maintenance diet had been removed from the aviary for approximately 1.5 h. On each trial birds were individually allowed to access the experimental set-up through the trap-window in the middle compartment and given access only to one of the three test compartments. A bowl containing powdered food (either 50.0 g of peanuts or 50.0 g of Macadamia nuts) was placed on the suspended platform in the accessible test compartment. Food in powdered form was used to prevent the bird from caching in the test compartments during the experience phase. The bird could freely eat and move between the middle compartment and the accessible test compartment during 15 minutes. At the end of a trial the bird was released into the outside aviary through the trap-window in the middle compartment. Birds were tested in the same order on all trials. The location and the type of food experienced by the birds on each trial changed according to two different patterns (Figs. 3.1 and 3.2). The test compartment that was accessible rotated on a 3-day basis, so that the birds that had access to compartment A on trial 1 experienced the test compartments in the following order across the nine trials: A-B-C-A-B-C-A-B-C. The kind of food available rotated on a 2-day basis, i.e. the same food was provided every other trial. As a result, all test compartments were experienced three times, and differed in the frequency in which they were associated with a specific type of food. In particular, two compartments were associated twice with one type of food and once with the alternative food, whereas the third compartment was characterized by the opposite pattern. The compartment that was accessible and the type of food available on trial 1 were counterbalanced across birds.

The test phase was conducted on the last day of the experience phase, approximately 3h after the ninth trial of the experience phase. Birds were again individually given access to the experimental set-up. All test compartments were accessible at this stage, and each contained one caching tray (5 x 3 pots filled with sand). A bowl containing 25 peanuts and 25 Macadamia nut halves, was placed in the middle compartment. Food items were arranged inside the bowl so that both types of food were equidistantly positioned from each opening that connected the middle compartment to the test compartments (Fig. 3.2). Birds could eat and cache both types of food in all test compartments for 15 minutes. At the end of the trial birds were released to the outdoor aviary through the middle compartment. Birds were not given the opportunity to recover their caches.

Analysis

I scored the number of items of each food type cached in the three test compartments. These data were collected at the end of each test trial by manually checking the caching trays. Data were analysed descriptively: I compared the caching patterns observed – both at the group level and at the individual level – with those predicted according to the Future Planning and Complementary Caching Hypotheses by inspecting the data plots.

Because the specific type of food and location experienced on the first experience trial were counterbalanced among the birds, the predictions about what to cache and where according to the two hypotheses were not identical for all individuals. To overcome this issue, and thus to facilitate the comparison between observed and expected caching patterns, raw data were sorted semantically. The three locations were relabelled such that: i) C1 corresponded to the compartment available on experience days 1, 4, 7, and to the hypothetical test on day 10; ii) C2 corresponded to the compartment available on experience days 2, 5, 8, and to the hypothetical trial on day 11; iii) C3 corresponded to the compartment available on experience days 3, 6, 9, and to the hypothetical trial on day 12. Similarly, the two types of food were relabelled such that: i) f1 corresponded to the food received on experience days 1, 3, 5, 7, 9 and on the hypothetical trial on day 11, and ii) f2 corresponded to the food received on experience days 2, 4, 6, 8 and on the hypothetical trial on days 10 and 12.

In addition to this descriptive analysis, data were also analysed statistically using a Bayesian approach (Appendix C). The Bayesian analysis was conducted in collaboration with Johanni Brea. The descriptive and statistical analyses yielded the same conclusions.

3.2.2: RESULTS AND DISCUSSION

Rome and Lima did not meet the criteria of the Pre-test in the first pair of trials nor when they were re-tested the second time. Thus, Rome did not proceed to the Familiarization. Due to a mistake, Lima did receive the Familiarization. Neither of these two birds proceeded to the test. In addition, Dublin showed very agitated behaviours during the Pre-test, consequently I stopped the testing of this bird on welfare grounds. Therefore, six birds in total passed the criteria of the Pre-test and proceeded to the Familiarization. All of these six birds passed the Familiarization and proceeded to the test (Tab. 3.1).

At the group level, the observed caching pattern appeared not to support the predictions of either hypotheses. The jays cached both types of food in all compartments, and allocated a seemingly comparable amount of each type of food across the three compartments (Fig. 3.3). Note that the evident disproportion between the total number of items cached for the two foods largely resulted from one bird (Caracas), who cached f1 exclusively, and in similar high quantities across the compartments (C1: 8 items; C2: 11 items; C3: 9 items). Thus, the apparent preference of the group toward f1 – the food that would have been absent, and so more desired on day 10 – is most likely an artefact of the data rather than a meaningful effect.

When caching patterns were analysed at the individual level, only the performance of one individual, Lisbon, was consistent with the Future Planning Hypothesis. In line with the Prediction 2, Lisbon cached f1 only in C1 and C3, while he cached f2 exclusively in C2 (Fig. 3.3). Therefore, this bird may have distributed the two types of food such that on the hypothetical following days both foods would have been available in all three compartments. The performance of all other birds however, seemed largely inconsistent with both hypotheses. Three birds (Caracas, Washington, Jerusalem) showed a caching pattern that was partially consistent with the Compensatory Caching Hypothesis: they cached the most items of f1 in compartment C2 and less in C1 and C3 (Fig. 3.3). Yet, these birds did not distributed f2 as predicted, such that their overall performance cannot be taken as evidence supporting the Compensatory Caching Hypothesis. Finally, the performance of the remaining two birds could not be interpreted according to any prediction. Wellington only cached f2 in C3, whereas Quito cached no item (Fig. 3.3).

Table 3.1: Number of items cached in Experiment 3.1. Raw data and semantically sorted data (C1 = compartment available on trials 1, 4, 7; C2 = compartment available on trials 2, 5, 8; C3 = compartment available on trials 3, 6, 9; f1 = food received on trials 1, 3, 5, 7, 9; f2 = food received on trials 2, 4, 6, 8). The entries in the Sequence column indicate the temporal order of compartments and food type during the familiarization, e.g. BCA-MP means that the bird was in compartment B on trials 1, 4 and 7 and received Macadamia nuts (M) on trials 1, 3, 5, 7 and 9.

		Raw Data						**Sorted Data**					
		A		**B**		**C**		**C1**		**C2**		**C3**	
Bird	**Sequence**	**P**	**M**	**P**	**M**	**P**	**M**	**f1**	**f2**	**f1**	**f2**	**f1**	**f2**
Washington	BCA-MP	4	2	2	2	3	3	2	2	3	3	2	4
Wellington	ABC-MP	0	0	0	0	1	0	0	0	0	0	0	1
Caracas	ABC-PM	8	0	11	0	9	0	8	0	11	0	9	0
Lisbon	CAB-MP	1	0	0	1	0	5	5	0	0	1	1	0
Jerusalem	BCA-PM	2	0	3	0	4	1	3	0	4	1	2	0
Quito	CAB-PM	0	0	0	0	0	0	0	0	0	0	0	0

Interestingly, all birds except Washington (and Quito, who cached no item) showed a pronounced preference for caching one of the two types of food: Caracas, 28/28 items f1; Lisbon 6/7 items f1; Jerusalem 9/10 items f1; Wellington, 1/1 f2 (Tab. 3.1).

In sum, the overall pattern of results did not provide support for either the Compensatory Caching Hypothesis or the Future Planning Hypothesis (see also Appendix C). One possible explanation for this inconclusive outcome is that the task imposed a too high cognitive load on the jays. To test between the two hypotheses in a scenario with a decreased cognitive load, I conducted a second experiment: here, the experience phase did not involve having access to one of the two foods on alternating days but either having access to one particular food or having access to no food.

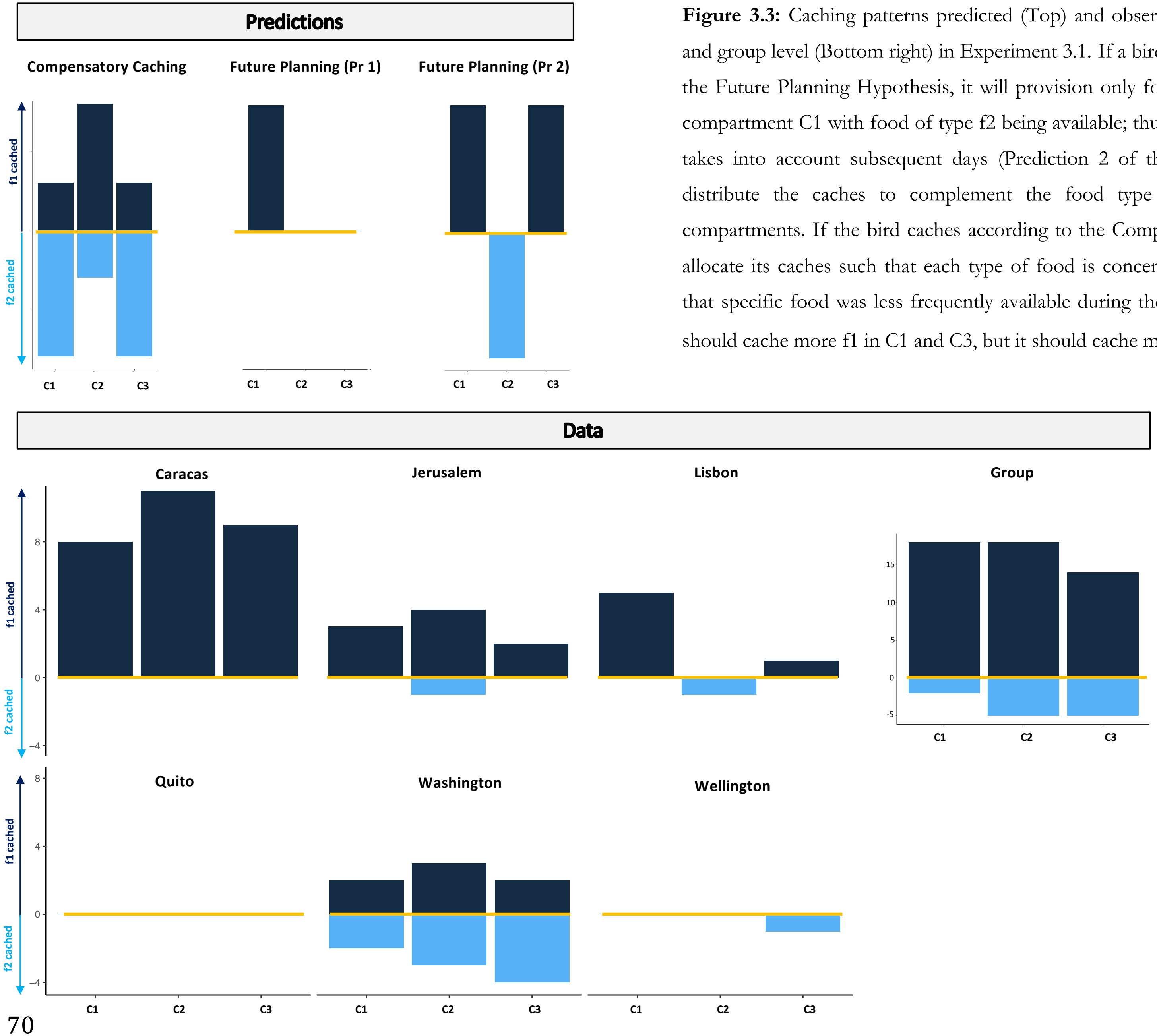

Figure 3.3: Caching patterns predicted (Top) and observed at the individual level (Bottom left) and group level (Bottom right) in Experiment 3.1. If a bird caches according to the Prediction 1 of the Future Planning Hypothesis, it will provision only for the next day when it expects to be in compartment C1 with food of type f2 being available; thus it would cache food f1 in C1. If it also takes into account subsequent days (Prediction 2 of the Future Planning Hypothesis), it will distribute the caches to complement the food type it expects to find in the respective compartments. If the bird caches according to the Compensatory Caching Hypothesis, it should allocate its caches such that each type of food is concentrated in those compartments in which that specific food was less frequently available during the Experience Phase. Therefore, the bird should cache more f1 in C1 and C3, but it should cache more f2 in C2.

3.3: EXPERIMENT 3.2

Experiment 3.2 employed the same protocol used in Experiment 3.1, but with one key difference: to decrease the cognitive load associated with the task, only one type of food (either peanuts or Macadamia nuts, depending on the individual bird) was used. Birds either received food (*Food* condition, F) or had access to no food (*No Food* condition, N) on alternating days during the experience phase. Like in Experiment 3.1, the test compartment that was accessible rotated on a 3-day basis. Food availability was rotated on a 2-day basis, i.e. food was available on every other trial.

This experiment was pre-registered on the Open Science Framework (https://osf.io/3y5tm/). The pre-registration was conducted after the pre-tests were completed but before the start of the test (i.e. prior to the first experience trial).

3.3.1: METHODS

Subjects

Eight birds (Colony 1, Appendix A) were tested in this experiment in October 2018. I tested all birds that had participated in Experiment 3.1 except Jerusalem: this bird was euthanized due to sickness unrelated to the behavioural tests, prior to the start of Experiment 3.2. All procedures were approved by the University of Cambridge Ethics Review Committee.

Experimental Set-up

The same set-up as in Experiment 3.1 was used.

Pre-test 1

Pre-test 1 was conducted to ascertain individual preferences for caching two different types of food. This information was used to decide which food would be provided to each individual bird in the test to minimise the probability that a bird would not cache during the test and thus minimise a decrease of the sample size. Approximately 1.5h after their maintenance diet had been removed from the aviary, birds were tested in visual isolation from the rest of the group, in an indoor compartment that was not part of the experimental set-up. Birds were provided with one caching tray and with two food bowls, one containing 50 peanuts, and one containing 50 Macadamia nut halves.

Birds were allowed to eat and manipulate (including caching in the compartment) the food for 15 minutes. At the end of the trial, birds were released back into the outdoor aviary. I manually checked the caching tray and recorded the number of items of each type of food cached. Approximately 3h after each trial, birds were again given access to the same compartment and were given the opportunity to retrieve their caches for 10 minutes. Retrieval sessions were conducted only to minimise the probability that birds would stop caching because this behaviour yielded no benefit to them. Each bird received three trials in total. Individual preferences were established by considering the type of food that was cached on average more often across the trials. To proceed to Pre-test 2, birds were required to have cached at least one food item in at least two of the three trials.

Pre-test 2

Eurasian jays tend to require repeated exposure to a food (even if they had previously received the same food) to start eating it. Given that the jays had not had the opportunity to consume powdered food following the completion of Experiment 3.1 (i.e. January-October 2018), it was necessary to ensure that the birds were still motivated to eat powdered food as this food was subsequently used in the test. To this end, Pre-test 2 was conducted to ascertain that birds would eat peanuts and Macadamia nuts in powdered form.

This Pre-test comprised two stages. In stage 1, birds were given the opportunity to eat both types of powdered food in the aviary as a group. Powdered peanuts and Macadamia nuts were presented in separate bowls, after the birds' maintenance diet had been removed from the aviary for approximately 1.5 h. Birds were observed by the experimenter from an observation hut adjacent to the aviary. If higher-ranking individuals monopolised the food bowls, they were separated from the group, such that lower ranking individuals could access the food. I scored the number of times each bird inserted their beak into each food bowl. To proceed to stage 2, birds were required to insert their beak at least twice into their preferred food (as determined in Pre-test 1). If this criterion was not reached by all birds on the first trial, the trial was repeated up to two times (i.e. a maximum of three trials in total).

In stage 2, birds were tested individually in an indoor compartment that was not part of the experimenter set-up and were provided only with their preferred food. Like in stage 1, birds were tested after their maintenance diet had been removed from the aviary for approximately 1.5h. The bird was allowed to eat freely from a bowl containing 50.0 g of their preferred food in powdered form for 15 minutes. Birds were required to eat at least 0.1 g of food to proceed to the Familiarization. If a bird did not pass this criterion, the trial was repeated up to two times (i.e. a bird received a maximum of three trials in total).

Familiarization

The Familiarization followed the same procedure as described in Experiment 3.1.

Test

The test followed the same procedure as in Experiment 3.1. However, instead of two foods, birds received only one food, i.e. their preferred food. This procedure was chosen to maximise the probability that each bird would eat the food during the test. Again, the experiment consisted of an experience phase (nine trials) followed by one test trial (Fig. 3.4). In the experience phase birds received one trial per day on nine consecutive days. The trials were conducted in the morning after the birds' maintenance diet had been removed from the aviary for approximately 1.5 h. On each trial birds were individually allowed to access the experimental set-up through the trap-window in the middle compartment and they were given access only to one of the three test compartments. On the platform was either a bowl containing 50.0 g of their preferred food in powdered form (*Food* condition, F) or an empty bowl (*No Food* condition, N). In the *Food* condition, food was available in powdered form to prevent the bird from caching in the test compartments during the experience phase. In the *No Food* condition, an empty bowl – rather than no bowl at all – was placed in the accessible compartment, both to ensure that it was only the availability of food that differed between the two conditions and to maximise the probability that the bird would enter the testing compartment when no food was available.

The bird could freely move between the middle compartment and the accessible test compartment and – in the *Food* condition – eat the food for 15 minutes. At the end of a trial, the bird was released into the outside aviary through the trap-window in the middle compartment. Birds were tested in the same order on all trials. Like in Experiment 3.1, the location and availability of food experienced by the birds on each trial changed according to two different patterns. The test compartment that was accessible rotated on a 3-day basis, so that the birds that had access to compartment A on trial 1 experienced the test compartments in the following order across the nine trials: A-B-C-A-B-C-A-B-C. The availability of food rotated on a 2-day basis, i.e. food was available every other trial. As a result, all test compartments were experienced three times, and differed in the frequency in which they were associated with the food. Specifically, two compartments were associated twice with the presence of food and once with the absence of food, whereas the third compartment was characterized by the opposite pattern. The compartment that was accessible on trial 1 and food availability were counterbalanced across birds. This meant that – as far as food availability is concerned – there were two group of birds: one group that experienced food on trial 1 (henceforth *Food-No Food* group, FN) and the other group that experienced no food on trial 1 (henceforth *No Food-Food* group, NF).

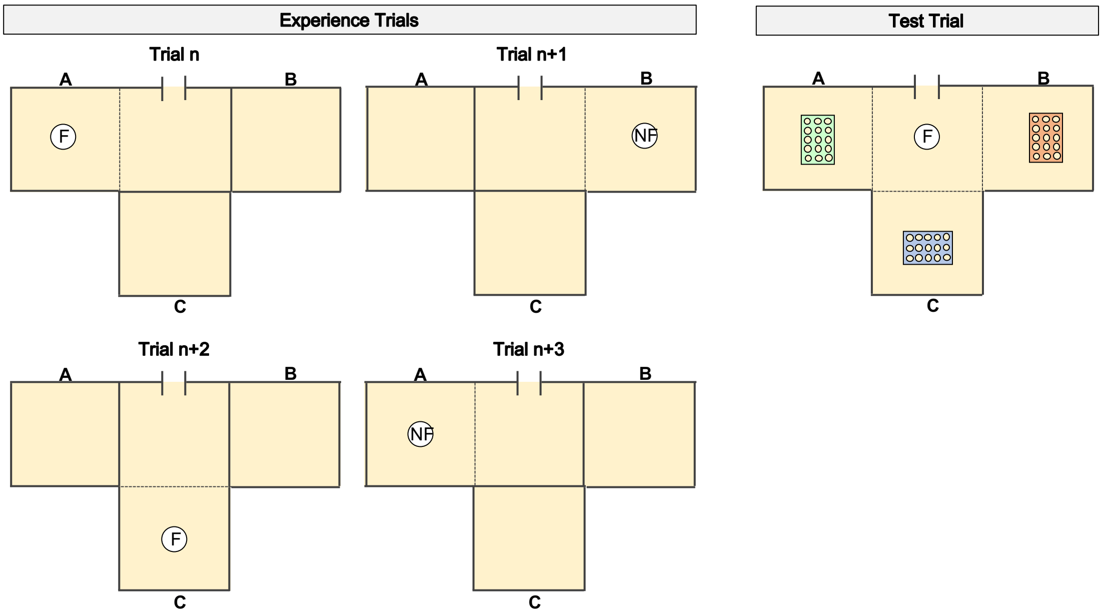

Figure 3.4: Top view of the experimental set-up of Experiment 3.2. Birds could access the three test compartments (A, B, C) from a middle compartment. On each experience trial (Left), the birds had access only to one test compartment (e.g. A in Trial n; B in Trial n+1), and they were presented either with a bowl containing powdered food (F, Trial n, Trial n+2) or with an empty bowl containing no food (NF, Trial n+1, Trial n+3). The compartment that was accessible and food availability rotated on a 3-days cycle and on a 2-days cycle, respectively. On the test trial (Right), a bowl containing food items (i.e. not food in powdered form) was placed in the middle compartment and caching trays were placed in all test compartment. Birds could freely move and cache in all compartments.

The test phase was conducted on the last day of the experience phase, approximately 3h after the ninth trial. Birds were again individually given access to the experimental set-up. All test compartments were accessible at this stage and each contained one caching tray (5 x 3 pots filled with sand). A bowl containing 50 items of the bird's preferred food (whole peanuts or Macadamia nut halves) was placed in the middle compartment. The bird could eat and cache the food in all test compartments for 15 minutes. At the end of the trial, the bird was released in the outdoor aviary through the middle compartment. Birds were not given the opportunity to recover their caches.

According to the Compensatory Caching Hypothesis birds should cache higher proportions of items in the compartment(s) where – during the experience phase – the food had been available only once than in the compartment(s) where the food had been available twice. Importantly, birds in the FN group experienced two compartments as being more frequently associated with food, whereas birds in the NF group experienced only one compartment as being more frequently associated with food. As result, the Compensatory Caching Hypothesis predicts that birds in FN group should cache more in one compartment, but birds in the NF groups should concentrate their caches equally across two compartments (Fig. 3.5).

In contrast, according to the Future Planning Hypothesis birds should cache more in the compartment(s) in which they expect to receive no food, either on the next day (hypothetical experience trial 10, Prediction 1) or on the following three days (hypothetical experience trials 10 to 12, Prediction 2). Both predictions are applicable to the FN group (Fig. 3.5). However, only Prediction 2 is relevant to the NF group. During the nine experience trials, these birds were given food every other day in the following sequence: N-F-N-F-N-F-N-F-N, thereby they would receive food in the hypothetical trial 10 and 12 but not in trial 11. As a result, if jays can cache according to future need, then it makes little sense for birds in the NF group to cache in the compartments where they expect to be on day 10 (Prediction 1) because food would be available anyway. Rather they should concentrate their caches only in the compartment in which they expect to be given access to on day 11 because this compartment would be the only one in which no food would be available among the three hypothetical trials (Prediction 2).

Analysis

I scored the number of items of food cached in the three test compartments. These data were obtained by manually checking the caching trays after the end of each trial. As in Experiment 3.1, data were analysed descriptively through the comparison between the caching patterns observed and those predicted according to the two contrasting hypotheses. Again, to facilitate the analysis, raw data were semantically sorted by using C1-C3 as variables in the plots. A distinction between f1 and f2 (as was done in Experiment 3.1) was not necessary because in this experiment each bird was provided with one type of food only.

In addition to this descriptive analysis, data were also analysed statistically using a Bayesian approach (Appendix C). The Bayesian analysis was conducted in collaboration with Johanni Brea. The descriptive and statistical analyses yielded the same conclusions

3.3.2: RESULTS AND DISCUSSION

All birds passed the Pre-tests and the Familiarization, except Dublin who did not pass the criterion in the Familiarization. Therefore, seven birds took part in the test. On the ninth and last experience trial, Lima went through a small empty space in between the suspended platform in the compartment and the mesh wall and therefore experienced not only the accessible compartment but also another one. Because this unforeseen circumstance may have influenced Lima's performance in the test trial, I decided to exclude him from further testing. Thus, six birds were tested in the test trial (Tab. 3.2).

The caching pattern recorded for the FN group violated the predictions of both hypotheses. According to the Future Planning hypothesis, birds should have concentrated their caches in C1 (Prediction 1), or in both C1 and C3 (Prediction 2), whereas following the Compensatory Caching hypothesis, they should have preferred C2 over C1 and C3 (Fig. 3.5). However, despite a slight preference toward C1, the FN group spread food items quite homogenously across the three compartments (Fig. 3.5). The same pattern also emerged for each bird in the FN group (Caracas, Washington, Quito) in the analysis at the individual level (Fig. 3.5).

Table 3.2: Number of items cached in Experiment 3.2. Raw data and semantically sorted data (C1 = compartment available on trials 1, 4, 7; C2 = compartment available on trials 2, 5, 8; C3 = compartment available on trials 3, 6, 9). The entries in the Sequence column indicate the temporal order of compartments and conditions during the familiarization, e.g. BCA-NF means that the bird was in compartment B on trials 1, 4 and 7 and received no powdered food (N) on odd days and powdered food (F) on even days.

		Raw Data			**Sorted Data**		
Bird	**Sequence**	**A**	**B**	**C**	**C1**	**C2**	**C3**
Caracas	BCA-FN	7	8	7	8	7	7
Washinghton	CAB-FN	2	2	3	3	2	2
Quito	ABC-FN	9	8	8	9	8	8
Wellington	CAB-NF	0	1	1	1	0	1
Rome	ABC-NF	6	3	7	6	3	7
Lisbon	BCA-NF	7	0	1	0	1	7

On the other hand, the performance of the birds in the NF group could not support the Future Planning Hypothesis, but it appeared – to some extent – compatible with the Compensatory Caching Hypothesis. In the line with the latter hypothesis, the analysis at the group level showed that birds cached more in C1 and C3 over C2 (Fig. 3.5). However, while similar number of items were expected to be cached in C1 and C3 under the Compensatory Caching Hypothesis, the group cached two times more items in C3 (15 items) than in C1 (7 items). The individual level analysis indicated that this pronounced preference toward C3 resulted from one bird, Lisbon, who cached 7 out of 8 items in C3. In contrast, the other two individuals of the NF group (Wellington and Rome) appeared to have fully met the prediction of the Compensatory Caching Hypothesis: they spread their caches uniformly across C1 and C3, and cached no items (Wellington) or a small fraction of items (Rome: 3/16 items) in C2 (Fig. 3.5).

Therefore, as in Experiment 3.1, the overall pattern of the results could not support either the Compensatory Caching Hypothesis or the Future Planning Hypothesis (see also Appendix C).

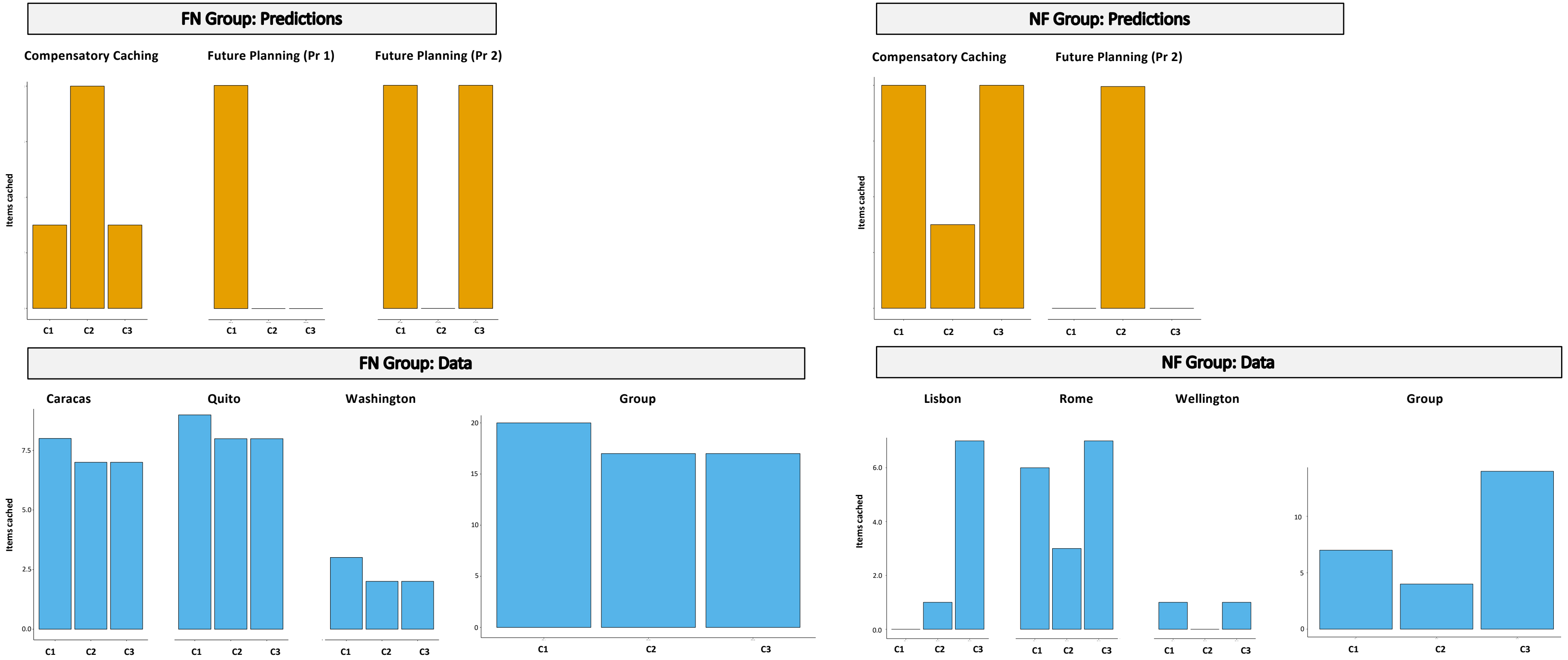

Figure 3.5: Caching patterns predicted (Top) and observed at the individual level and group level (Bottom) in Experiment 3.2. A bird in the FN group should expect to not receive powdered food on test day 10. If it caches according to Prediction 1 of the Future Planning Hypothesis, it will provision only for the next day, when it expects to be in compartment C1 with no food available; thus it would cache exclusively in C1. If it takes into account the next three days (Prediction 2 of the Future Planning Hypothesis), it will distribute the caches in compartments C1 and C3. If the bird caches according to the Compensatory Caching Hypothesis the bird should cache more in compartment C2, where it has only once encountered the powdered food. In contrast, a bird in the NF group should expect to receive food on the hypothetical trial 10 (and 12), but not on trial 11. Therefore, according to Prediction 2 of the Future Planning Hypothesis, it should cache in C2, whereas following the Compensatory Caching Hypothesis, it should preferentially cache in C1 and C3. Note that Prediction 1 of the Future Planning Hypothesis is not applicable to the NF because the birds in this group should expect to receive food on trial 10.

3.4: GENERAL DISCUSSION

In this chapter the objective was to evaluate two alternative hypotheses about future planning, focussing on the cognitive mechanism underpinning corvids' ability to cache for the future. To this end, I tested Eurasian jays in two experiments in which the Compensatory Caching and the Future Planning hypotheses would have opposite predictions. Across both experiments, the data did not support either hypothesis.

In Experiment 3.1, the performance of a single bird (Lisbon) was compatible with one of the two hypotheses: Lisbon's caching patterns was in line with the Prediction 2 of the Compensatory Caching Hypothesis. Thus, this bird might have distributed his caches such that in the hypothetical following trials, both types of food would have been available in each compartment. On the other hand, in Experiment 3.2, two birds (Wellington and Rome) cached as predicted by the Compensatory Caching Hypothesis. Specifically, they cached comparably more items in the two compartments in which the food was less frequently available during the experience phase.

Inter-individual differences are not rare in comparative cognition, particularly in studies focussing on complex abilities (e.g. Seed et al., 2006, 2009b; see also Chapter 2). Hence, the fact that only a few individuals cached as predicted does not *per se* disprove that Eurasian jays are endowed with the cognitive mechanisms described by the two hypotheses. For instance, the individuals tested in this study might differ in their ability to plan for the future, with Lisbon being endowed with higher cognitive sophistication than the others. However, inter-individual difference can also be caused by chance or other factors that are not related to cognitive variability (e.g. motivation). Because individual jays were given a single test trial in both Experiment 3.1 and 3.2, it is hard to tear apart which factor may have produced the observed variability within each experiment. Yet, when the overall pattern of results is taken into account, it appears more likely that three individuals met one of the predictions in a single trial, due to chance. First, because the performances of Lisbon, Rome and Wellington were not compatible with the same hypothesis, results would suggest that caching in Eurasian jays should be underpinned by both the ability to plan for the future and a predisposition to distribute caches according to location-specific weights. This possibility cannot be excluded a priori, yet, hinging on two different mechanisms, it is less parsimonious than the Compensatory Caching or the Future Planning hypotheses alone. Second, if the caching performance of Lisbon, Rome and Wellington was actually the expression of the cognitive mechanisms described by one of the two hypotheses, then these individuals should have consistently met the predictions of one hypothesis in both experiments. In contrast, Lisbon failed to cache according to the Future Planning Hypothesis in Experiment 3.2, while Wellington did not cache as predicted by the Compensatory Caching Hypothesis in Experiment 3.1. Because Rome only took part in Experiment 3.2, no consideration can be made for this individual. Therefore, the overall pattern of results cannot be taken as evidence that corvids' caching behaviour is underpinned by either of the two cognitive mechanisms that were investigated. Note that the Bayesian analysis of the data (Appendix C) support the same conclusion.

Interestingly, birds most frequently spread their caches among all compartments in both experiments. Considering all individual trials in which at least one item was cached (i.e. 5/6 trials in Experiment 3.1; 6/6 trials in Experiment 3.2), birds distributed their caches across the three compartments in 8 out of 11 eleven trials. This is particularly evident in the performance of Caracas and Washington, both of whom consistently cached similar quantities of items in the three locations (Fig. 3.3 and 3.5). Thus, location-specific experience before the test might not have played a key role in guiding birds' decisions about *where* to cache. A similar argument may be raised in regard to the decision about *what* to cache. Indeed, in Experiment 3.1 (when two foods were available) most birds showed a pronounced preference to cache only one type of food, regardless of whether that food would have been unavailable in the next days or had less frequently been associated in the past with the compartments where it was eventually cached.

Taken together, the results reported in this chapter seem to be in contrast with previous studies in corvids. In particular, Raby et al. (2007) found that, when California scrub-jays were allowed to cache in two different locations – one in which food has been consistently available and one in which it had not – they tended to concentrate their caches in the location where food has been absent in the past. Raby et al. (2007) further reported that, when allowed to cache two types of food, scrub-jays distributed their caches heterogeneously such that each food was cached preferentially in the location in which the alternative food had been experienced. Regardless of whether these performances were achieved through an ability to plan for the future or by attributing location-specific weights, Raby et al. (2007)'s study suggests that scrub-jays decide where and what to cache on the basis of their previous experience about food availability in multiple locations. In this study I could not find equivalent evidence.

Given that the experiments reported here and those conducted by Raby et al. (2007) employed different paradigms, it is not possible to draw conclusive inferences about what factors may have caused inconsistent results in the two studies. To this end, a crucial first step for future research is to replicate the findings reported in this chapter in Eurasian jays, and those obtained by Raby et al. (2007) in California scrub-jays. Subsequently, in case the results of both studies will be corroborated, future work should investigate the factors (e.g. experimental paradigms, model species) that may have caused inconsistent outcomes between these two studies.

One factor that future research may focus on is whether methodological differences may have influenced the ecological validity of the tasks, and consequently affected jays' capability to cache according to future needs. A key difference between the studies is that the association between food and locations was stable across experience trials in Raby et al. (2007)'s experiments but it changed systematically in the experiments reported here. It is possible that the two kinds of manipulations may have affected the ecological relevance of the task. For a wild corvid, it may be more plausible to encounter locations in which food is consistently available during a given period than to experience locations in which a specific food is abundant every few days in a cyclic fashion. For instance, Eurasian jays are specialized cachers that primarily rely on trees' fruits (i.e. acorns) as food for caching (de Kort and Clayton, 2006; Goodwin, 1951). It may be more likely for a wild jay to experience a scenario resembling the paradigms of Raby et al. (2007) than those employed here. An oak tree does not bear abundant fruits every few days but no fruits in between; rather it consistently bears acorns over weeks, in one season. Therefore, future work on the cognitive mechanisms underpinning caching behaviour in corvids may want to evaluate the interplay between experimental designs and ecological validity of the task. To this end, it would be also beneficial to take into account species-specific differences in caching given that these features may influence the ecological relevance of the tasks for different species.

The methodological difference between studies that was noted above further highlights that the paradigms I have employed likely imposed a higher cognitive load on the jays, relatively to Raby et al. (2007)'s paradigms. However, in their current form, neither the Compensatory Caching Hypothesis nor the Future Planning Hypothesis involve any auxiliary claims regarding the extent of information that the underlying mechanism is able to process. The Future Planning Hypothesis specifies that individuals should be able to keep track of 'what-where-when' representations to select actions that are most appropriate at a given point. Thus, the cognitive load involved in this study – namely the need to integrate information about food availability at three different locations based on time intervals – seems compatible with the hypothesis. Similarly, the Compensatory Caching Hypothesis specifies that the suitability of a given caching location for a specific food is based on food-specific 'weights' associated with each location, which are updated when the bird finds itself at that location. Thus, in its current form the Compensatory Caching Hypothesis also seems compatible with the cognitive load required in Experiments 3.1 and 3.2. Future theoretical work may, however, expand the hypothesis regarding the manner in which the 'weights' are updated, and thus should motivate further empirical work.

In summary, the data from this study provide no support for either of the two tested cognitive abilities being the base of future-oriented caching behaviour in Eurasian jays (see also Appendix C). In the first part of this chapter, I introduced a third explanation that has been proposed in the literature, namely the Mnemonic Association Hypothesis. To evaluate whether this third hypothesis could provide a better explanation for the Eurasian jays' caching behaviour future studies could utilise equivalent procedures that can simultaneously test between different competing hypotheses. In addition, future studies replicating the experiments reported here both in Eurasian jays and other corvid species are needed to strengthen the claims that can be made based on the current findings.

In parallel to future planning and problem solving, there is a third cognitive domain in which corvids appear to excel, namely social cognition. As summarized in Chapter 1, a number of studies have suggested that corvids, and Eurasian jays in particular, may respond to different types of mental states, such as perspectives and desires of others. In Chapter 4, I shall attempt at gaining further insight into the cognitive sophistication of Eurasian jays by focusing on their social cognition.

CHAPTER 4:

Can Eurasian jays integrate cues about others' desires and perspectives to protect their caches?

Abstract

In Chapter 2 and 3, I explored the cognitive sophistication of Eurasian jays by focusing on their abilities to solve physical problems and plan for the future, respectively. As discussed in Chapter 1, a third cognitive domain in which corvids have been reported to show remarkable complexity is social cognition. Corvids appear to be capable of adjusting their behaviour according to another's perspective, knowledge and desire. For example, Eurasian jays seem to employ a variety of cache protection strategies to minimise cache loss by either responding to the visual or auditory perspective or the desire of an observing conspecific. Yet, it is an open question whether these jays (or any other corvid) can integrate cues about different kinds of mental states and perform the optimal response accordingly. In this chapter I investigate whether Eurasian jays can limit the risk of cache loss by accounting simultaneously for cues about the desire and perspective of a potential conspecific pilferer. Hinging on established paradigms, I conducted two experiments in which both the visual perspective and the desire of an observer jay were manipulated. Opaque and transparent barriers were used to manipulate the observer's visual access to cache locations, whereas the observer's desire towards different types of food was manipulated through specific satiety. In Experiment 4.1, the jays could hide only one type of food – either the same food the observer was sated on or a different food – but could choose to distribute their caches across locations that were in-view and out-of-view for the observer. In Experiment 4.2, jays could only cache in one location (either in-view or out-view for the observer) but could choose between two types of cacheable foods: one that was currently desired and one that was not currently desired by the observer. Consistently, across both experiments the jays' caching pattern provided no evidence that they could integrate information about the observer's desire and perspective. Thus, the integration of these mental states may be too cognitively demanding for Eurasian jay, or alternatively such ability may have a limited applicability to real-life caching contexts.

4.1: INTRODUCTION

In the first two experimental chapters of this thesis I explored the cognitive sophistication of the Eurasian jay by focusing on physical problem solving (Chapter 2) and future planning abilities (Chapter 3). In this chapter I turn my attention to social cognition and report a study investigating whether Eurasian jays can simultaneously respond to cues about different mental states of another agent, namely the agent's perspective and desire.

Theory of Mind – a set of abilities allowing individuals to attribute internal, mental states to others – is what enables humans to explain, predict, and even manipulate, the behaviour of other individuals. The reason why this set of abilities is referred to as a *Theory* of Mind is that it provides a causal framework within which different observable entities can be used to infer otherwise imperceptible mental states. Theory of Mind (ToM) appears to develop as a step-wise process: children around the age of two, seem to first develop the ability to acknowledge others' perspective (Moll and Tomasello, 2006), while subsequently, between three to five years of age, they appear to progressively acquire the abilities to explicitly reason about others' desires, and then knowledge and beliefs (Wellman and Liu, 2004). Evidence suggests that this developmental trajectory is stable across cultures (although minor differences exist, Selcuk et al., 2018; Wellman et al., 2006) and transcends sensory modalities, e.g. both visual and auditory cues can be used to reason about others' mental states (Hasni et al., 2017). Despite this stepwise development, different ToM abilities are subsumed into a flexible cognitive framework that allows us not only to process a single type of social information but also to integrate different types of information at a given time. Adult humans routinely make inferences about the behaviour of another agent by simultaneously taking into account different types of mental states such as others' perspective, desires and beliefs (e.g. Baker et al., 2017).

Interestingly, humans' capability to integrate multiple pieces of social information emerges during infancy, prior to the full development of ToM. For instance, infants younger than two years old can integrate an adult' emotional expressions and referential cues (e.g. gaze direction, body orientation), and use it to adjust their behaviour toward a target (Moses et al., 2001; Repacholi et al., 2014). Crucially, such sophisticated cognitive processing may not entail the representation of mental states:

infants may implicitly register social cues and exhibit adaptive responses accordingly without an explicit understanding of another person's behaviour (Apperly and Butterfill, 2009; Butterfil and Apperly, 2013).

According to some authors, the evolution of ToM is tightly linked to the emergence of some of the most iconic human traits, such as language and a pervasive culture (Heyes and Frith, 2014; Lohmann and Tomasello, 2003). Yet a growing body of research raises the possibility that non-human animals may take into account the perspectives, desires, knowledge and beliefs of conspecifics and adjust their behaviours accordingly (e.g., primates: Buttelmann et al., 2017; Drayton and Santos, 2014; Flombaum and Santos, 2005; Kano et al., 2019; Krupenye and Call, 2019 dogs: Horowitz, 2011; Maginnity and Grace, 2014; corvids: Bugnyar et al., 2016; Dally et al., 2006; Ostojić et al., 2013; Shaw and Clayton, 2012). Note however that it is debated whether the mechanisms underpinnings these flexible behaviours in non-human animals really hinge on the attribution of mental states to conspecifics or whether they entirely rely on observable behavioural cues (Heyes, 2015, 2017; Penn and Povinelli, 2007b; Whiten, 2013). Studies of ToM in non-human animals most frequently employed paradigms in which individuals had to solve a task by responding to a single type of mental state (e.g. desires) of another agent. In contrast, testing the ability to simultaneously process different types of mental states has been largely overlooked in animals. As a result, very little is known about whether – like humans – other species can integrate multiple social cues that correlate with others' mental states and exhibit appropriate responses accordingly. Corvids, and Eurasian jays in particular, are an ideal candidate for this line of research because they appear to be capable of responding – independently – to social cues correlating with different types of mental states.

As discussed in Chapter 1, several studies have reported that jays flexibly employ a variety of anti-pilfering strategies to limit the risk of cache loss. In the presence of a conspecific, California scrub-jays and Eurasian jays tend to cache in less visible locations (e.g. behind barriers, in shadow areas), or in non-noisy substrates, thus suggesting they respond to the visual or to the acoustic perspective of a potential pilferer (Dally et al., 2005; Legg and Clayton, 2014; Shaw and Clayton, 2013; Stulp et al., 2009). In parallel, research investigating food sharing behaviour indicated that jays may be able also to attribute desires to conspecifics. Male Eurasian jays choose which kind of food to cater to their mates, on the basis of females' desires (Ostojić et al., 2013, 2014). According to a recent study, jays' ability to respond to others' desires may not be limited to food sharing behaviour, rather it may extend also to caching. Ostojić et al., (2017) tested whether jays will adjust the amount of caching of two distinct foods according to what an observer, a potential pilferer, was pre-fed on. The authors found that the jays tend to cache more of the food the observer was pre-fed on, i.e. the food that was less desired by the observers, and thus less likely to be pilfered. However, cachers exhibited the same caching pattern regardless of whether or not they had witnessed the pre-feeding of the observer, thus suggesting that the observer's behaviour during caching played an important role in the cacher's decision making process and may be sufficient to explain the food-sharing behaviour of the males (Ostojić et al., 2017). Building on this evidence, a critical question is whether jays, like humans, can integrate multiple cues that correlate with different types of mental states to flexibly solve social problems.

In this chapter I investigate whether Eurasian jays can integrate information about a conspecific's perspective and current desire to selectively protect those caches that are at most risk of being pilfered. Hinging on previously established paradigms (Legg and Clayton, 2014; Ostojić et al., 2017), I conducted two experiments in which I manipulated the observers': i) visual perspective of caching locations by allowing cachers to hide food either behind an opaque or a transparent barrier, and; ii) desire toward different types of food through specific satiety. In Experiment 4.1, jays were provided with only one type of food – either the same food the observer was previously sated on, or a different food – and two caching trays, one that the observer could see and one that the observer could not see. Jays could choose whether to cache in-view or out-view of the conspecific. In contrast, in Experiment 4.2, jays were provided with a single caching tray – which could either be seen by the observer or could not be seen by the observer – and two types of food, one of which had previously been pre-fed to the observer. Jays could decide whether to cache the same type of food on which the observer had been sated or the different food. Thus, the designs of the two experiments were complementary, such that jays could most effectively protect their caches by deciding *where* to cache in Experiment 4.1, and *what* to cache in Experiment 4.2.

4.2 EXPERIMENT 4.1: Do jays protect their caches by choosing where to cache?

4.2.1 METHODS

Subjects

Nine Eurasian jays (four males and five females) were tested: Caracas, Lima, Lisbon, Dublin, Rome, Jerusalem, Wellington, Washington and Quito. These were all the birds available at the time of testing. Birds were housed as a group (Colony 1, Appendix A) in a large outdoor aviary (20x10x3 m) at the Sub-Department of Animal Behaviour, University of Cambridge, Madingley. Outside of testing the birds had *ad libitum* access to their maintenance diet of vegetables, eggs, seed and fruits. Water was available at all times. All procedures were approved by the University of Cambridge Animal Ethics Committee. The experiment was conducted in October-November 2017.

Experimental set-up

Birds were tested in indoor testing compartments (2x1x3 m) that were accessible from the aviary through flap windows. During the Familiarisation, each bird was tested in isolation, i.e. with no other birds present in the test room. Compartments used during the Familiarisation were not used in the test phase. During the test, a cacher bird and an observer bird were located in adjacent compartments. These compartments were separated by opaque sheeting except for a mesh window (30x55 cm) through which the birds had visual access to the adjacent compartment.

Each compartment contained a suspended platform (1x1 m) approximately 1 m from the ground, onto which food bowls, caching trays and Perspex barriers could be placed. The bowls contained i) a handful of maintenance diet (MD); ii) 50 Macadamia nut halves (M), or; iii) 50 whole peanuts with skin (P). Each type of food was presented in a bowl of a specific colour, and these colours were kept consistent for all birds. Rectangular seedling trays (5 x 3 pots filled with sand) were used as caching trays. Trays were painted different colours and were trial-specific to minimise the probability that birds' caching behaviour in one trial would be influenced by its memory from previous trials. A Perspex barrier – which was placed next to the caching trays in the cacher's compartment – was used to manipulate the observer's visual access to the caching trays. To give cachers the option to cache in or out of view of the observer, I used a 'T-shaped' barrier – henceforth T-barrier – consisting of three plastic sheets (25x40 cm) forming two arms and one stem. This was the same barrier that was used by Legg and Clayton (2014). One arm of the 'T' was constructed out of transparent Perspex, while the other arm and the stem were constructed out of white opaque Perspex. This T-barrier was placed around two caching trays (Fig. 4.1) such that the observer could see the tray behind the transparent arm (*in-view* tray) but could not see the tray behind the opaque arm (*out-of-view* tray). Due to the height of the barrier, the observer could always see the cacher when the latter was standing upright in proximity of the trays. However, the observer could not see the location where the cacher hid the food when it was caching in the *out-of-view* tray.

General Procedure

To ensure that the birds were mildly hungry and thus likely to interact with food provided during testing, their maintenance diet was removed from the aviary approximately 1.5h prior to testing. Test trials involved a pre-feeding phase followed by a caching phase. Before the start of the trial, two birds (one cacher and one observer) were given access to two adjacent compartments. Subsequently, I placed a bowl containing pre-feeding food (Macadamia nuts or peanuts) on the suspended platform in the observer's compartment and a bowl containing a handful of maintenance diet on the platform in the cacher's compartment. Both bowls were placed in front of the mesh window (Fig. 4.1) to ensure that the birds could see each other whilst eating and to maximise the chances that the cacher could see on which food the observer was pre-fed. I then left the test room and the birds could eat the pre-feeding food for 15 minutes. Next, I entered the test room again and removed the bowls as well as any food remains on the platforms. In the subsequent caching phase, I positioned the caching trays, as well as the barrier and the food bowl, in front of the mesh window in the cacher's compartment (Fig. 4.1). I then left the test room and the birds were given 15 minutes, during which the cacher could eat and cache the food in the trays. At the end of the trial, I opened the flap windows to allow the birds to re-join the rest of the group in the aviary and recorded the amount of food eaten and the number and location of caches in the trays. Approximately three hours after each trial, the cacher was allowed to re-enter the caching compartment. At this stage, the flap window was kept open so that the bird had access not only to the indoor compartment but also to the adjacent outside run. Note that the door connecting the outside run to the aviary was kept closed, thus no other bird could enter the cacher's run or compartment. During 10 minutes, the cacher could retrieve the hidden items and re-cache them in the compartment and in the adjacent small outdoor run. Observers were not present during recovery. This retrieval phase was conducted only to reduce the probability that birds would stop caching in the trays so that these data were not analysed. Birds received a single test trial per day.

Familiarization

Birds received two Familiarization trials on two separate days to ensure that they were comfortable caching in trays when these were placed in proximity of each of the two arms of the T-barrier. I presented the birds with the T-barrier, a single caching tray and a food bowl. On each trial, birds were given the opportunity to eat and cache for 15 minutes. On each trial, the tray was placed either behind the opaque or the transparent arm of the T-barrier. The order in which birds experienced the tray in the two locations was counterbalanced across birds. The orientation of the barrier within the compartment was different from that later used during testing, and kept consistent for each bird across the two Familiarization trials (Fig. 4.1). The type of food (Macadamia nuts or peanuts) was randomly assigned to birds but each bird was provided with the same type of food in both trials. To proceed to testing, birds had to cache at least one item on each trial.

Test

During the pre-feeding phase, cachers could see a conspecific eating a specific type of food: either the same type of food they were going to receive in the subsequent caching phase or a different one. In the subsequent caching phase cachers were provided with the same food used in the Familiarization and with two caching trays, each one placed behind one of the two arms of the T-barrier (Fig. 4.1).

All birds were tested in two conditions (one trial per condition) that differed in whether or not the type of food provided to the observer in the pre-feeding phase matched the type food provided to the cacher in the caching phase (Fig. 4.1). In the *High Desire* Condition, the type of food provided to the cacher and to the observer differed (e.g. M for the observer, and P for the cacher). In the *Low Desire* Condition, the same type of food was used (e.g. P for both the observer and cacher). The order in which the cachers experienced the *High Desire* and *Low Desire* conditions was counterbalanced across birds.

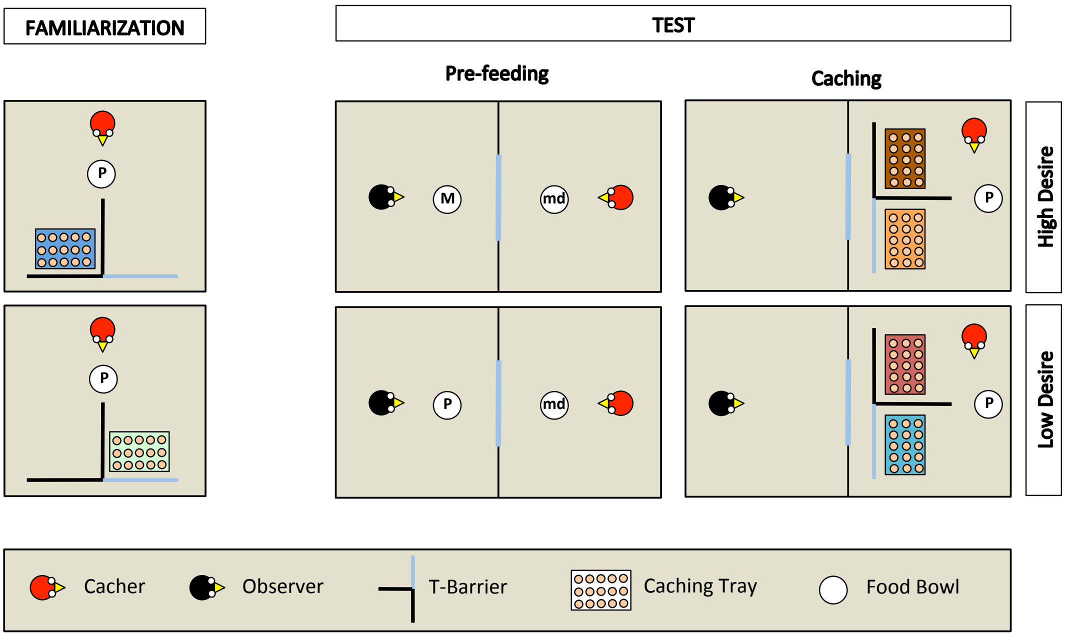

Figure 4.1: Top-view schematic representation of the set-up and procedure used in Experiment 4.1. In the Familiarization (left panels), the cacher bird received two trials, one in which the caching tray was placed near the opaque arm of the barrier (top panel), and one in which the tray was placed near the clear arm of the barrier (bottom panel). In the test, trials were composed by a pre-feeding phase (middle panels) and a caching phase (right panels). The cacher bird received two trials that differed in the type of food that was provided to the observer bird in the pre-feeding phase. In one trial (*High Desire* Condition, top panels), the food provided to the observer in the pre-feeding phase differed from the food the cacher bird could subsequently cache. In the other trial (*Low Desire* Condition, bottom panels), the food provided to the observer in the pre-feeding phase was the same as the food the cacher bird could subsequently cache. In the pre-feeding phase of both trials, the cacher bird was provided with a handful of maintenance diet (md). Note that, for explanatory purposes, the scheme shows the cacher as being provided with peanuts (P) in the Familiarization and in the caching phase of the two test trials. However, in the experiment, cacher birds were randomly assigned to one type of food (either peanuts, or Macadamia nuts), which was used consistently in the familiarization and in the caching phase of all trials.

Analysis

In each individual test trial, I recorded the number of food items cached in each tray. I then calculated the difference in the number of items cached in the *out-of-view* tray minus the number of items cached in the *in-view* tray. This difference score [$\text{Caches}_{\textit{out-of-view}}$ – $\text{Caches}_{\textit{in-view}}$] represents an indication for a preference to cache in the *out-view* tray over the *in-view* tray. I compared this difference between the two conditions using a Wilcoxon signed rank test. In addition, in the *High Desire* condition, I used a one-sample Wilcoxon signed rank test to compare the difference in the number of items cached in the *out-view* tray minus the number of items cached in the *in-view* tray against chance. I also recorded i) the number of items taken from the bowl by observers (during pre-feeding) and by cachers, and ii) the number of items recovered by cachers during recovery sessions. These data were not relevant to the experimental question, such that they were not analysed. Statistical analyses were performed in R (R.3.5) using the RStudio 1.1.447 wrapper (RStudio Team, 2018). Alpha was set to 0.5.

If the jays can integrate information about the observer's perspective and desire, their caching pattern should meet two predictions. First, the difference in the number of items cached in the *out-of-view* tray minus the number of items cached in the *in-view* tray should be higher in the *High Desire* condition than in the *Low Desire* condition. This is because it is in the *High Desire* condition that the observer has a stronger desire toward the cacher's food, so that the cacher would have to protect their caches more carefully. Second, in the *High Desire* condition, the cacher should exhibit a clear preference for caching in the *out-of-view* tray, therefore in this condition the difference score should be higher than expected by chance.

4.2.2 RESULTS AND DISCUSSION

All birds except two (Lisbon and Dublin) reached the criterion in the Familiarization and therefore seven birds proceeded to the test. The differences between the items cached out-of-view and in-view did not differ between the *High Desire* Condition and the *Low Desire* Condition (Wilcoxon Signed Rank Test: N=7, W=9, p=0.40; Fig. 4.2). Therefore, in contrast to the first prediction, the jays did not preferentially cache items in the *out-of-view* tray when the observers had a higher motivation to pilfer that specific food. Further, in the *High Desire* condition the difference in the number of items cached in the *out-of-view* tray minus the number of items cached in the *in-view* tray did not differ from chance (One-sample Wilcoxon Signed Rank Test: N=7, W=-7, p=0.61). Thus, contradicting the second prediction, the jays did not prefer to cache in the *out-of-view* over the *in-view* tray when they had access to a food that was highly desired by the observer.

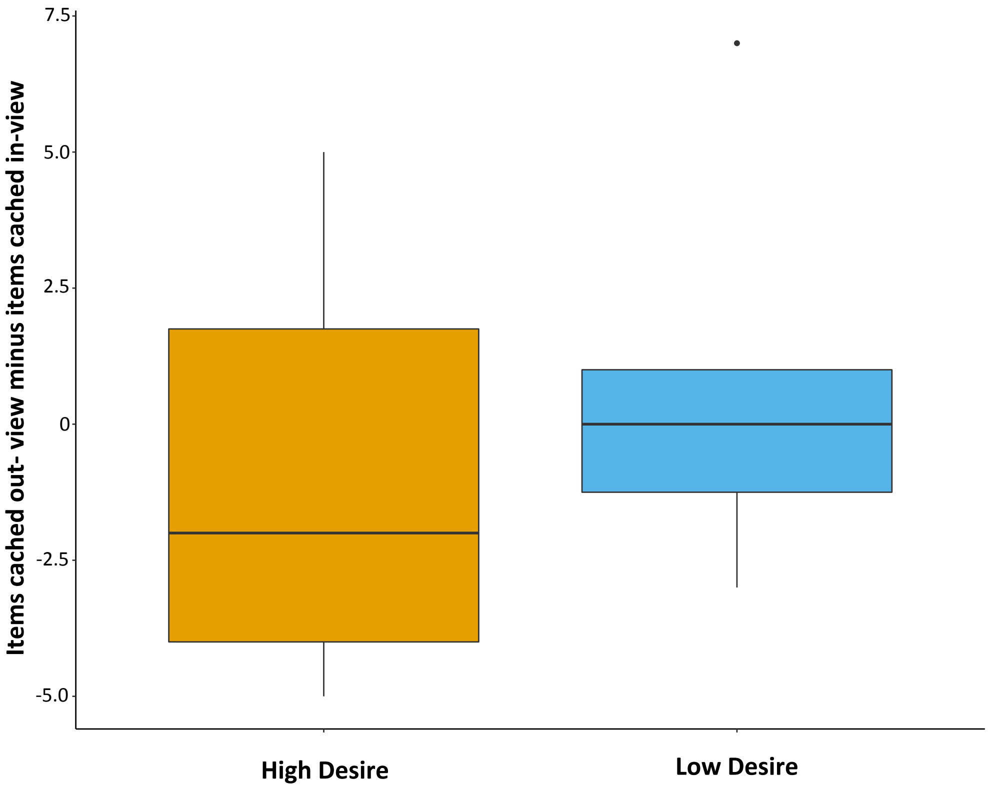

Figure 4.2: Box and whisker plot of data in Experiment 4.1. The plot shows the difference in the number of items cached in the *out-of-view* tray minus the number of items cached in the *in-view* tray in the two experimental conditions. In the *High Desire* condition (orange), the food cached by the cacher bird differed to the food on which the observer was sated. In the *Low Desire* condition (blue), the food cached by the cacher bird was the same as the food on which the observer was sated on.

Taken together, the results of this experiment are not consistent with the possibility that jays can integrate cues about the perspective and desire of a conspecific to most effectively protect their caches. Surprisingly however, these results also appear incompatible with previous studies reporting that Eurasian jays flexibly adjust their caching behaviour on the basis of an observer's perspective (Legg and Clayton, 2014). In particular, Legg and Clayton (2014) reported that jays tended to cache more in the *out-of-view* tray when a conspecific was present than when they cached in private. Although Experiment 4.1 employed the same procedure (including the same T-barrier) as the observed condition in Legg and Clayton (2014) – the only difference being in the food provided to cachers[8] – I found no indication that jays preferentially cached in the location that was not visible from the observer's perspective.

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[8] In Legg and Clayton (2014)'s experiment, the jays were provided with 30 peanut halves. In contrast, in Experiment 4.1 I presented the jays with either 50 Macadamia nut halves or 50 whole peanuts with skin.

4.3: EXPERIMENT 4.2: Do jays protect their caches by choosing what to cache?

To further investigate whether jays can integrate cues that correlate with another's perspective and desire, I conducted a second caching experiment based on a complementary design. Here, on each trial, cachers were presented with two types of food but with a single caching tray. Thus, I tested whether jays could minimize the risk of their food being pilfered by adjusting *which* type of food to cache – rather than *where* to hide it, as in Experiment 4.1 – according to the observer's different desire toward the two foods and according whether the observer had visual access to the caching location.

4.3.1 METHODS

Subjects

Eight Eurasian jays (Colony 1, Appendix A) participated in this experiment. All individual birds that had taken part in Experiment 4.1 were tested, except Dublin who showed signs of distress during the Familiarization of Experiment 4.1 and was therefore excluded from further testing. The experiment was conducted in January-February 2018. All procedures were approved by the University of Cambridge Ethics Review Committee.

Experimental set-up

I used the same set-up described in Experiment 4.1 except that here I manipulated the observer's visual access using an 'U-shaped' barrier – henceforth U-barrier. This barrier consisted of two lateral Perspex sheets (26x25 cm) and one central Perspex sheet (53x25 cm) forming two angles of approximately 45°. The U-barrier was positioned around one caching tray: in one condition the barrier was transparent and in the other it was opaque (Fig. 4.3).

Individuals were randomly assigned to one type of food, which was consistently used in all Familiarization and test trials.

General Procedure

I used the same procedure described in Experiment 4.1.

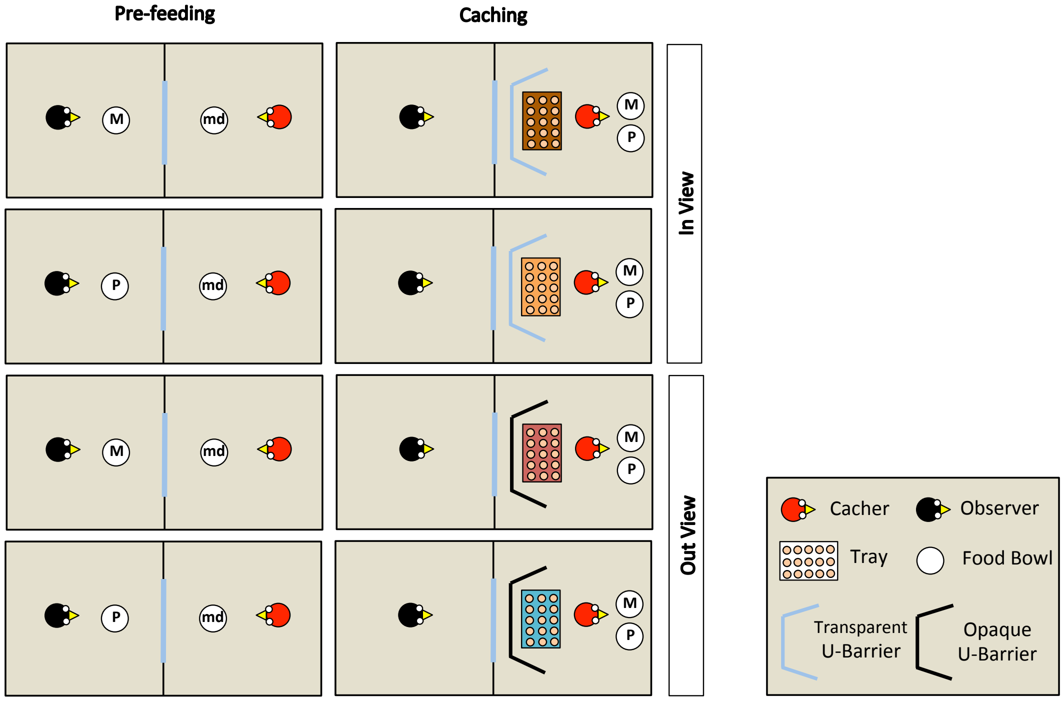

Figure 4.3: Top-view schematic representation of the set-up and procedure used in the test of Experiment 4.2. Trials were composed by a pre-feeding phase (left panels) and a caching phase (right panels). The cacher bird received two trials with the transparent U-barrier (*In-view* condition, top panels), and two trials with the opaque U-barrier (*Out-of-view* condition, bottom panels). Within each condition, trials differed in the type of food (either peanuts, P, or Macadamia nuts, M) that was provided to the observer in the pre-feeding phase. The cacher bird was always presented with a handful of maintenance diet (md) in the pre-feeding phase of all trials.

Familiarization

Familiarization trials were conducted to ascertain that birds were comfortable in caching both types of food (Macadamia nuts and peanuts) in a tray placed in proximity of each of the barriers. Birds received two trials on separate days. On each trial, birds were presented with the U-barrier, a single caching tray and two food bowls, which were presented sequentially. Birds were given the opportunity to eat and cache for 20 minutes: during the first 10 minutes they were provided with one type of food and during the next 10 minutes with the other. The order in which the birds experienced the two types of foods was counterbalanced across birds and across trials, such that each bird experienced one order on their first trial and the opposite order on their second trial. On each trial, birds were presented with one type of the U-barrier: opaque or transparent. The order in which the birds experienced the two types of the U-barrier was counterbalanced across birds. To proceed to testing, birds had to i) cache at least one item on each trial, and ii) cache at least one item of each kind of food across the two trials.

Test

Following the general structure of Experiment 4.1, in the pre-feeding phase cachers were first able to see an observer feeding on one specific type of food (Macadamia nuts or peanuts). In the subsequent caching phase, cachers were provided with a single tray that was placed within the U-barrier, and with two food bowls, one containing 50 Macadamia nut halves and one containing 50 whole peanuts with skin. All birds were tested in two conditions that differed in the feature of the barrier (Fig. 4.3). In the *In-view* condition, the transparent U-barrier allowed the observer to see the caching tray. In the *Out-of-view* condition, the opaque U-barrier prevented the observer from seeing the caching tray. In each condition, the birds received two trials, one in which the observer was pre-fed on one type of food (e.g. Macadamia nuts), and one in which the observer was pre-fed the other type food (e.g. peanuts). Birds first received both trials of one condition, and then the two trials of the other condition. The order in which the two conditions were conducted was counterbalanced across birds. The order in which observers were pre-fed with the two kinds of food within a condition was counterbalanced across birds, but kept consistent across conditions such that the order of the two trials was the same in both conditions. If a bird did not cache any item in one or two trials, those trials were repeated at the end of the experiment. However, if a bird did not cache any items in more than two trials, that bird was not tested any further and was excluded from the analysis.

Analysis

I recorded the number of items cached in the tray on each trial. For each individual, I calculated the difference in the number of peanuts cached and the number of Macadamia nuts cached. This difference score [$P_{cached} - M_{cached}$], which represents an indication of a preference to cache P over M, was compared between the two trials within the *In-view* and the *Out-of-view* conditions using a Wilcoxon signed-rank test.

I further calculated a difference of difference scores, namely in each condition, I subtracted the difference score of the trial in which the was observer pre-fed M from the difference score of the trial in which the observer was pre-fed P: $[P_{\text{cached}} - M_{\text{cached}}]_{\text{pre-fed P}} - [P_{\text{cached}} - M_{\text{cached}}]_{\text{pre-fed M}}$. The difference of difference scores represents an indication of a preference to cache P over M when the observer was sated on P relative to when the observer was sated on M. This variable was compared between conditions using a Wilcoxon signed-rank test. Like in Experiment 4.1, I also recorded i) the number of items taken from the bowl by observers (during pre-feeding) and by cachers, and ii) the number of items recovered by cachers during recovery sessions. Again, these data were not relevant to the experimental question, so that they were not analysed. Statistical analyses were performed in R (R.3.5) using the RStudio 1.1.447 wrapper (RStudio Team, 2018). Alpha was set to 0.5.

If the jays can integrate information about the observer's perspective and desire, they should cache in line with the following two predictions. First, the jays should exhibit a higher difference of difference scores in the *In-view* condition than in the *Out-of-view* condition. This is because it is in the *In-view* condition that the caches are at a higher risk of being pilfered and thus caching the food that is less desired by the observer would decrease this risk. Second, in the *In-view* condition, the cacher should show a clear cache-protection strategy: the difference score (as an indication for a higher preference to cache P over M) should be higher when the observer is sated on P than when the observer is sated on M.

4.3.2 RESULTS AND DISCUSSION

All birds except one (Lisbon) reached the pre-specified criteria in the Familiarization and thus seven birds proceeded to the testing phase. The difference of difference scores (i.e. the indicator for a preference to cache P over M when the observer is sated on P relatively to when the observer is sated on M) did not differ between the *In-view* and *Out-of-view* conditions (Wilcoxon Signed Rank Test: $N=7$, $W=-4$, $p=0.80$). Therefore, in contrast to the first prediction, the jays did not cache more items of the type of food that was less desired by the observer, when caches were at higher risk of being pilfered (i.e. *In-view* Condition). I further found that in both conditions the difference scores (differences between the number of peanuts and Macadamia nuts cached) did not differ between when the observers were pre-fed peanuts and when they were pre-fed

Macadamia nuts (*In-view* condition, Wilcoxon Signed Rank Test: N=7, W=-3, p=0.86; *Out-of-view* condition, Wilcoxon Signed Rank Test: N=7, W=-1, p=1; Fig. 4.4). Thus, in contrast to the second prediction, the jays did not protect their caches by hiding a larger amount of the same food that the observer had been sated on when the caching tray were visible to the conspecifics.

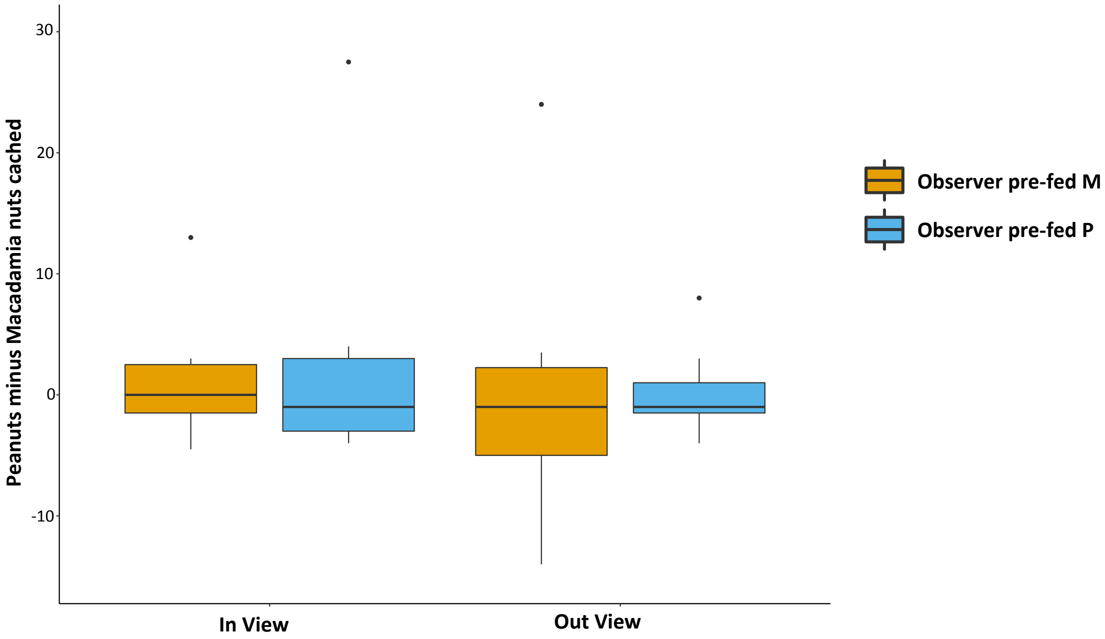

Figure 4.4: Box and whisker plot of data in Experiment 4.2. The plot shows the difference in the number of peanuts cached minus the number of Macadamia nuts cached for each condition. In the *In-view* condition, the observer had visual access to the caching tray, whereas in the *Out-of-view* condition, the observer did not have visual access to the caching tray. The colour of the boxes in the plot differs on the basis of the type of food that was provided to the observer in the pre-feeding phase: blue denotes that the observer had been pre-fed P and orange denotes that the observer had been pre-fed M.

Overall, these results appear to closely match those in Experiment 4.1. As in the previous experiment, the observed caching pattern does not support the possibility that Eurasian jays are capable of integrating cues about the perspective and desire of another. Second, the results are also inconsistent with a previous report indicating that Eurasian jays can adjust their caching by responding to another agent's desire. Ostojić et al. (2017) reported that when allowed to cache in the view of a conspecific, jays preferentially cached the type of food that was less desired by the observer over the type of food that was more desired by the observer. In contrast, I did not find equivalent evidence in the condition where the U-barrier was transparent, which – apart from the presence of the barrier – followed the same procedure as that reported in the Seen condition of the study by Ostojić et al. (2017).

4.4: GENERAL DISCUSSION

I this chapter I investigated whether Eurasian jays can integrate cues correlating with others' desires and perspective and perform the most advantageous caching strategy accordingly. I found no evidence that the jays were capable of integrating the cues of these different mental states. Specifically, in Experiment 4.1, jays did not preferentially cache in the *out-of-view* tray when they were provided with a food that was highly desired by the observer, and not more than when the food was not desired by the observer. Consistent with this result, in Experiment 4.2, jays did not preferentially cache the food for which observers had a decreased desire, and not more when the observer could see them than when they could not see them. Thus, on the whole, the results suggest that jays may not be able to integrate the cues about the observer's perspective and desires.

It is possible to raise the argument that jays' capability to employ clear cache protection strategies may have been impaired by the increased cognitive requirements of the experimental designs. An important consideration here is that in this study I used experimental manipulations of the observer's perspective and desire that – when applied separately, i.e. when only one of the observer's mental states was manipulated – yielded a behavioural response from cachers that could be interpreted as a cache-protection strategy. A second consideration is that whenever an individual is supposed to process cues correlating with different mental states of another social agent – either through mental-state attribution and/or 'behaviour-reading' – the cognitive load imposed is inevitably increased. Thus, the lack of a behavioural response by cachers in this study – if supported by further evidence for non-integration in future studies – may be showing up the limits of jays' information processing ability, at least in the caching context. If this is the case, then jays' cognition may only be sufficiently flexible to allow the processing of one type of cue correlating with another individual's mental state at a given time.

It has been suggested that corvids evolved large brains and complex cognition independently from primates, yet in response to comparably challenging social and ecological environments (Emery and Clayton, 2004; see also Chapter 1). In this regard, the social demands of caching, such as the need to limit cache loss due to pilfering, are considered to have played a key role in corvids' cognitive evolution (de Kort and Clayton, 2006). If this is case, then the cognitive challenges imposed by caching may have not have exerted sufficient pressures – at least in Eurasian jays which do not live in stable large groups (Goodwin, 1951, 1986) – for the evolution of a cognitive machinery allowing to integrate different kinds of mental states. Perhaps the processing of single mental state at a given time is sufficient to foster effective cache protection strategies in this species. A relevant parallel here may be provided by Bray et al. (2014)'s discussion of the differences in perspective taking abilities between lemurs and monkeys. In a food-stealing task lemurs appear to account for the visual perspective of a competitor but, unlike macaques (Santos et al., 2006), they do not seem to respond to the competitor's acoustic perspective (Bray et al., 2014). This finding led the researchers to hypothesize that – when compared to lemurs – the monkeys experienced a more complex social environment which may have posed a need for more sophisticated perspective taking abilities (Bray et al., 2014).

The jays' apparent inability to simultaneously respond to multiple types of mental states (as reported in this chapter) should also be considered in the light of the ecological validity of tasks. Eurasian jays form territorial pairs but do not live in large and stable flocks (Goodwin, 1951, 1986) so that they may have limited opportunity to perceive variation in desires for different types of food in conspecifics that are not sexual partners. It is therefore possible that the need to respond to subtle variations in the desires of competitors may have not played a key role in the cognitive evolution of this species. Yet this capability may have been far more relevant in the food sharing context. Supporting this view evidence that Eurasian jays can adjust their behaviour according to others' desires appears substantially more solid in the cooperative food sharing context than in the competitive caching context (Ostojić et al., 2013, 2014, 2016, 2017). Thus, it cannot be excluded that jays may have failed to respond to both the perspective and desire of a potential pilferer not because they are incapable of integrating different social cues *per se*, rather because the ability to respond to behavioural cues that correlate with desires, and consequently the need to integrate this social information with the perspective of a conspecific, may have a reduced applicability in real-life caching scenarios. Two complementary approaches may be used to investigate this possibility. On the one hand, a food-sharing task could be designed to test whether Eurasian jays can account simultaneously for the perspective and desire of pair mates. On the other hand, one may investigate whether jays can adjust their caching strategy by integrating a different pair of mental states.

In contrast with previous literature, I found no indication that Eurasian jays employed cache protection strategies based on one social cue alone, namely that jay responded to either the perspective or the desire of a conspecific. Specifically, in Experiment 4.1 jays did not – in the *High Desire* condition, i.e. when cached food was desired by the observer– show a preference for caching in the *out-of-view* tray. This is what would have been expected given the result reported by Legg and Clayton (2014): the authors found that jays preferred to cache in the *out-of-view* tray in the presence of a conspecific but not when in private. Similarly, in Experiment 4.2 jays did not – in the *In-view* condition, i.e. when the observer could see the cache location – show a preference for caching the food on which the observer was sated on and thus for which they should have had a decreased desire. This is what would have been expected given the results reported by Ostojić et al. (2017): the authors reported that jays showed a higher preference for caching food A over food B when the observer was sated on food A than when the observer was sated on food B. These inconsistencies between the evidence reported in this chapter and those of previous studies are particularly surprisingly given the similarities in the paradigms used. In the caching phase of the *High Desire* condition (Experiment 4.1), I employed the same procedure used by Legg and Clayton (2014) in the *Observed* condition. Note however, the food used differed between the studies. Further, the procedure of Experiment 4.2 closely matched that used by Ostojić et al. (2017) in the Seen condition, with the exception that in the latter study, there was no transparent barrier between the caching tray and the observer's compartment. From a logical and theoretical perspective, there seems to be no valid reason why this minor difference in the set-up would affect jays' ability to respond to a conspecific's perspective and desire. Thus, a crucial question raised by this study is to what extent previously reported effects are actually robust and reliable. Quantifying the repeatability and replicability of the original behavioural effects may be beneficial for future studies before progressing to the next questions. It may be useful for future research to acquire more detailed information about the behaviours of the observer and cacher birds during the testing. In particular, it would be interesting to score whether, at the time when the cacher bird hides the food in the tray, the observer bird is positioned such that it can actually see the caching location and whether it is paying attention to the caching event (Brecht, 2017). Accounting for the variability in the observers' behaviour may help clarifying the inconsistencies between different studies.

In sum, this study failed to provide evidence that Eurasian jays are able to selectively protect those caches that are at most risk of being pilfered by processing simultaneously information about the perspective and desire of a conspecific. Hence jays' social cognition may not be flexible enough to allow the integration of different cues correlating with different types of mental states, unlike human Theory of Mind. Yet further investigation is needed to corroborate this view. Particularly interesting would be to test jays' ability to integrate others' desire and perspective in the food sharing context, as well as investigating whether jays' caching strategies can account for the simultaneous processing of alternative types of mental states.

Before the issue of whether jays can integrate different kinds of social cues is addressed in future studies, I think it is essential to corroborate the previously reported effects that I could not provide support for in this study, i.e. that Eurasian jays flexibly adjust their caching behaviour according to another's visual perspective and according to another's desires. To this end, in Chapter 5 I report a replication of the study by Legg and Clayton (2014). In addition, I also report an investigation into the robustness of the effect reported by Ostojić et al. (2017) by testing whether a minor difference in the set-up (i.e. presence or absence of a transparent barrier) may have caused the inconsistent results between the original study and Experiment 4.2.

CHAPTER 5:

Caching tactics based on another's current desire or visual perspective: how robust is the evidence in Eurasian jays?

Abstract

In Chapter 4 I found no indication that Eurasian jays were capable of responding simultaneously to the visual perspective and current desire of another bird to effectively protect their caches. Unexpectedly, the results of these experiments were also at odds with those reported in previous studies. Specifically, Experiment 4.1 did not support the finding reported by Legg and Clayton (2014) that Eurasian jays cache predominately behind an opaque barrier over a transparent barrier when observed by a conspecific than when in private. In parallel, Experiment 4.2 could not corroborate the results reported by Ostojić et al. (2017), namely that Eurasian jays prefer to cache a type of food that had been eaten to satiety by a conspecific over a food that had not been eaten by a conspecific. In this chapter I aim to gain further insight into the results of the previous chapter by testing the robustness and reliability of the effects reported by Legg and Clayton (2014) and Ostojić et al. (2017). In Experiment 5.1 I conducted a replication of Legg and Clayton (2014)'s study with a different group of birds to those used in the original study. Here, I found no evidence that jays adjusted their caching pattern according to the visual perspective of a conspecific. In Experiment 5.2 I explored whether the inconsistencies between the results in Experiment 4.2 and those in Ostojić et al. (2017)'s experiment may have been caused by a minor difference in set-up, namely the presence or absence of a transparent barrier. Here, the results showed that the barrier had no effect on the jays' caching behaviour, and crucially that birds showed no preference for caching the same type of food that the observer had been sated on over another type of food. The results of these two experiments are in line with the negative findings reported in Chapter 4, thus challenging the robustness of the effects reported by Legg and Clayton (2014) and Ostojić et al. (2017), and raising the possibility that these studies yielded false positive results.

5.1: INTRODUCTION

In Chapter 4 I investigated whether Eurasian jays can simultaneously take into account the visual perspective and current desire of a conspecific to most effectively protect their caches. Consistently across two experiments, data provided no indication that jays can adjust their caching behaviour by integrating different types of social cues. Surprisingly however, the results were also incompatible with previously reported effects, namely that jays adapt their caching pattern according to *either* the visual perspective *or* the current desire of a potential pilferer (Legg and Clayton, 2014; Ostojić et al., 2017).

In particular, Legg and Clayton (2014) investigated whether Eurasian jays strategically select caching locations to reduce the risk of pilfering by conspecifics. Legg and Clayton (2014)'s experiment encompassed three conditions: jays could cache when an observer bird – either a higher ranked individual (*Observed by dominant* condition) or a lower ranked individual (*Observed by subordinate* condition) – was housed in an adjacent compartment, or when no conspecific was present (*Private* condition). Jays were given the opportunity to cache in two locations that differed as to whether they could or could not be seen from an adjacent compartment and thus by the observer bird (if and when present). To this end, the cacher jays were presented with a T-barrier (Chapter 4) and two caching trays, one positioned behind the opaque arm of the barrier (*out-of-view* tray) and one positioned behind the transparent arm of the barrier (*in-view* tray). The authors compared the jays' caching pattern in the *Private* condition with that in the *Observed* conditions[9], and found that jays cached proportionately more items in the *out-of-view* tray in the presence of a conspecific than when caching in private. Thus, jays appeared to have adjusted their caching behaviour according to the visual perspective of the observer, and strategically preferred to cache in a location that could not be seen by the observer to reduce the risk of pilfering. If the effect reported by Legg and Clayton (2014) is robust, then it is reasonable to predict that a preference toward caching in the *out-of-view* tray should also be detected when jays' performance is analysed *within* the *Observed* condition. In contrast with this prediction, in Experiment 4.1 I gave Eurasian jays the opportunity to cache in two trays while a conspecific was present, finding that the jays did not cache more than expected by chance in the tray that could not be seen

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[9] In Legg and Clayton (2014)'s study the two *Observed* conditions were merged together due to no difference in the cachers' behaviour between when the observer was subordinate and when they were dominant.

by the observer.

Ostojić et al. (2017) investigated whether Eurasian jays and California scrub-jays can attribute desires to a conspecific that is not a pair-mate, and protect their caches by strategically caching the type of food that the observer was not currently motivated to pilfer. In the experiment, a cacher and an observer jay were housed in adjacent testing compartments. In the pre-feeding phase, the observer could feed to satiety on a specific type of food: maintenance diet in the baseline trial, and either food A or B on each of the two test trials. In the *Seen* condition, the cacher could witness the pre-feeding of the observer, whereas in the *Unseen* condition, a curtain was lowered in between the two compartments so that the cacher could not see the observer's pre-feeding. In the subsequent caching phase, cacher jays were given the opportunity to cache both food A and B in the view of the observer. The authors found that, relatively to the baseline trial, jays' preference for caching food A over food B was larger after the observer had eaten food A to satiety than after the observer had eaten food B to satiety. Hence, jays appeared to have adjusted their caching strategy on the basis of the current desire of a conspecific, and cached predominantly the type of food that was less desired by the observer. This caching strategy was exhibited consistently within both conditions – i.e. regardless of whether the cacher had seen or had not seen which particular food had been provided to the observer – thus indicating that the observer's behaviour at the time of caching may have played a key role in the decision-making process of the cacher. Note that, when data were re-analysed by considering only the performance of Eurasian jays (n=7), the effect was still significant in the *Seen* condition – although it was not significant in the *Unseen* condition (Crosby, 2019). In contrast with Ostojić et al. (2017), in Experiment 4.2 I found that – if allowed to cache in a location that was visible to an observer bird (*In-view* condition) – Eurasian jays did not prefer to cache a type of food that was not currently desired by an observer over a food that was highly desired by an observer.

As discussed in Chapter 4, the procedures I have employed in Experiments 4.1 and 4.2 were very similar to those devised by Legg and Clayton (2014) and Ostojić et al. (2017), respectively. Specifically, Experiment 4.1 and Legg and Clayton (2014)'s test involved the same procedure apart from the type and quantity of the food that was provided to the cachers. Similarly, the *In-view* condition of Experiment 4.2 and the *Seen* condition of Ostojić et al. (2017)'s experiment employed the same procedure, with the exception that in the former study the observers could see the caching location through a transparent barrier, whereas in the latter study no barrier was present. Therefore, in the light of the methodological similarities between the studies it is challenging to explain the inconsistencies between the results reported in Chapter 4 and in the previous studies.

The aim of this chapter is gain further insight into the unexpected outcomes of the experiments in Chapter 4 by testing the robustness and reliability of two caching strategies reported in Eurasian jays, namely to i) preferentially cache in locations that cannot be seen by a conspecific, and ii) preferentially cache a type of food that is currently not desired by a conspecific. Specifically, in Experiment 5.1 I attempt at reproducing the finding reported by Legg and Clayton (2014) by conducting a direct replication of the original study. In Experiment 5.2 I investigate whether the presence or absence of a transparent barrier – i.e. the minor difference in the set-up between Experiment 4.2 and Ostojić et al. (2017)'s experiment – affect Eurasian jays' capability to cache by responding to another's current desire.

5.2: EXPERIMENT 5.1

5.2.1 METHODS

Subjects

Two colonies of adult Eurasian jays were tested. Colony 1 was formed by eight birds (four females, four males): Caracas, Lima, Lisbon, Dublin, Rome, Wellington, Washington and Quito. These were the same individuals that participated in the experiments reported in Chapter 4. All birds in Colony 1 took part in the experiment. Colony 2 was formed by seven birds, five of which could be used for testing (two males, three females): Hoy, Romero, Hunter, Webb, and Adlington. The remaining two birds of Colony 2 were excluded a priori because they regularly exhibited agitated behaviour when inside individual testing compartments. Birds in Colony 2 participated in the original study by Legg and Clayton (2014). Three of the birds that took part in the original study (i.e. Hoy, Hunter, and Adlington) were also tested here. Thus, 13 birds (eight from Colony 1, five from Colony 2) participated in Experiment 5.1. I tested the birds in Colony 1, while Rachael Crosby tested birds in Colony 2.

Each colony was housed in a large outdoor aviary (20x10x3 m) at the Sub-Department of Animal Behaviour, University of Cambridge, Madingley. The aviaries housing the two colonies were largely similar (e.g. size, gravelly soil), yet they differed in the location and material of perches (wood or metal poles). In addition, testing compartments were indoor areas for Colony 1, whereas they were outdoor areas delimited by wooden walls and covered by a roof for Colony 2. Outside of testing the birds had *ad libitum* access to their maintenance diet of vegetables, eggs, seed and fruits. Water was available at all times. All procedures were approved by the University of Cambridge Animal Ethics Committee. The experiment was conducted in October-December 2018.

Experimental set-up

Birds were tested in testing compartments (2x1x3 m) that were accessible from the aviary through flap windows. During the Pre-test, each bird was tested in private, i.e. with no other birds present in the test area. Compartments used during the Pre-test were not used in the test phase. During the test, birds could cache in private (*Private* Condition) or while being observed by a conspecific (*Observed* Condition). In the latter condition, a cacher bird and an observer bird were located in adjacent compartments. Compartments were separated by opaque sheeting except for a mesh window (30x55 cm) through which the birds had visual access to the adjacent compartment.

Each testing compartment contained a suspended platform (1x1 m) approximately 1 m from the ground, on which caching trays, Perspex barriers, and food bowls could be placed. Rectangular seedling trays (5 x 3 pots filled with sand) were used as caching trays. Trays were painted different colours and were trial-specific to minimise the probability that birds' caching behaviour in one trial would be influenced by its memory from previous trials.

The same Perspex barrier used in Experiment 4.1 and in Legg and Clayton (2014)'s study was used here to manipulate the observer's visual perspective of the caching trays. The T-barrier consisted of three plastic sheets (25x40 cm) forming two arms and one stem. One arm of the 'T' was made out of transparent Perspex, while the other arm and the stem were made out of white opaque Perspex. The T-barrier could be placed around two caching trays (Fig. 5.1), such that the observer could see the tray behind the transparent arm (*in-view* tray) but could not see the tray behind the opaque arm (*out-of-view* tray). Due to the height of the barrier, the observed could always see the cacher when the it was standing upright in proximity of the trays. However, the observer could not see the location where the cacher hid the food when it was caching in the *out-of-view* tray.

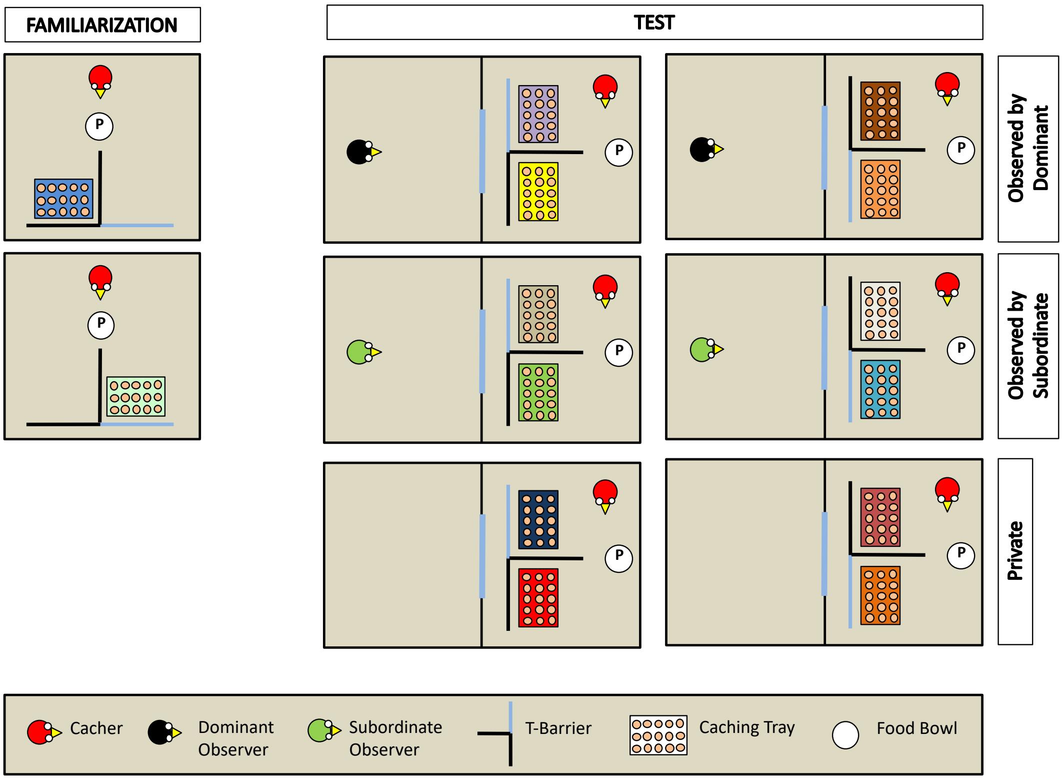

Figure 5.1: Top-view schematic representation of the set-up and procedure used in Experiment 5.1. In the Familiarization (left panels), the cacher bird received two trials, one in which the caching tray was placed near the opaque arm of the barrier (top panel), and one in which the tray was placed near the clear arm of the barrier (bottom panel). In the test (central and right panel), birds were tested in three conditions: *Observed by dominant*, *Observed by subordinate*, *Private*. In each condition, cachers received two trials that differed in the orientation of the T-barrier.

General Procedure

To ensure that the birds were mildly hungry and thus likely to interact with food provided during testing, their maintenance diet was removed from the aviary approximately 1.5h prior to each trial. Before the start of the trial, a bird (i.e. the cacher) was given access to the testing compartment where the caching tray(s) and the T-barrier had already been positioned. In the test trials of the *Observed* condition, a second bird (i.e. the observed) was also induced to enter the adjacent compartment. Subsequently, a bowl containing 30 peanut halves was placed on the suspended platform in the cacher's compartment. The experimenter then left the test room and the cacher was given the opportunity to eat and cache food during 15 minutes. Next, the experimenter entered again in the test room and released the bird(s) in the outdoor aviary. At the end of the trial, the experimenter recorded the amount of food eaten and the number and location of caches.

Approximately three hours after each trial, the cacher was allowed to re-enter the caching compartment. During 10 minutes, the cacher could retrieve the hidden items and re-cache them in the compartment and in the adjacent small outdoor aviary. Observers were not present during recovery. This retrieval phase was conducted only to reduce the probability that birds would stop caching in the trays. Birds received a single test trial per day.

Dominance Hierarchy

In Legg and Clayton (2014)'s experiment, cacher birds received four trials in the *Observed* condition: two trials in which they were observed by a higher ranked individual (*Observed by dominant* condition), and two trials in which they were observed by a lower ranked individual (*Observed by subordinate* condition). Thus, to replicate the original design it was necessary to determine the dominance hierarchy within each aviary. To this end, *ad libitum* observations were conducted for each colony. Birds were observed while as a group in the outdoor aviaries, after they were deprived of food for approximately 2h. For each observation session, maintenance diet was presented on a single food platform in the aviary. The identity of birds involved in any displacement (i.e. bird x approaches bird y causing bird y to leave) was recorded. To solicit competitive interactions among birds, higher value food items (e.g. wax worm larvae) were also presented in a bowl or scattered around on the floor of the aviary. If necessary, higher ranked birds were locked into separate compartments to favour interactions among low ranked birds. Observation sessions were conducted on multiple days, until data allowed to establish a clear social hierarchy within the colonies. Sessions lasted approximately 40 min each.

Pre-test

A Pre-test was conducted to ascertain that the birds were comfortable to cache in proximity of both the transparent and the opaque arm of the T-barrier. Birds received two trials, on separate days. Testing occurred in private, i.e. no other bird was present in the adjacent compartment. On each trial, the bird was presented with a bowl containing 30 peanuts halves, the T-barrier and a caching tray, which was placed in proximity of either the transparent or the opaque arm of the barrier. The cacher could eat and cache for 15 minutes; subsequently it was allowed to re-join the rest of the group in the aviary.

The order in which birds were given the two trials was counterbalanced among birds, so that half of the birds could cache in proximity of the opaque arm of the barrier on the first trial, whereas the remaining birds could cache close the transparent arm on the first trial. The position of the barrier (e.g. opaque arm facing left) was counterbalanced among birds, but kept consistent between multiple trials received by the same individual. The compartments used in the Pre-test were not used in the subsequent test. In addition, the T-barrier was positioned differently within the compartment during the Pre-test and the test (Fig. 5.1). These procedural precautions were set to ensure that the birds were not more familiar with one of the two orientations of the barrier (e.g. opaque arm facing left) during the test.

To proceed to the test, birds were required to cache at least one item in each of the two Pre-test trials, i.e. birds had to cache at least one item when the tray was placed in proximity of both the transparent and also when the opaque arm of the barrier. If no item was cached in a trial, then that trial was repeated for a maximum of three times. Thus, a bird could receive a maximum of 6 trials in total. The repeated trials were conducted at the end: for example, if a bird's first trial had to be repeated, then the bird received the second, pre-planned trial on day 2, and subsequently it received the first trial again on day 3.

Test

Following Legg and Clayton (2014), the experiment encompassed three conditions. In the *Private* condition, the cacher could eat and cache when no other bird was present. In the *Observed by dominant* condition, the cacher was given the possibility to eat and cache while a higher ranked individual of the groups was present in the adjacent compartment. In the *Observed by subordinate* condition, the cacher could cache while a lower ranked individual was housed in the adjacent compartment.

On each trial, the cacher was given access to the testing compartment and presented with the T-barrier, the *in-view* tray (i.e. the tray placed behind the transparent arm of the barrier), the *out-of-view* tray (i.e. the tray placed behind the opaque arm of the barrier) and a bowl containing 30 peanuts halves. The bowl was placed close to the stem of the 'T' such that it was equidistant from the two caching trays (Fig. 5.1). The cacher could eat and cache for 15 minutes and was subsequently released back into the aviary.

In each condition, birds received two trials, which differed in the orientation of the T-barrier. In half of the trials, the opaque arm of the barrier was facing the outdoor aviary, whereas, in the other half of the trials it was facing the opposite direction. Each bird was first tested in all conditions with the barrier being kept consistent in one specific orientation, subsequently it received the remaining trials with the barrier being kept consistent in the alternative orientation. The order in which the two orientations of the barrier were experienced, was counterbalanced among birds. All birds were tested in all three conditions, except the highest and lowest ranked bird in each colony. The formers could only be tested in the *Private* and *Observer by subordinate* conditions. On the other hand, the latter could only be tested in the *Private* and *Observer by dominant* conditions. Thus, most birds received six trials (two trials per condition), whereas the highest and lowest ranked individuals in each colony received only four trials because they could only be tested in two of the three conditions.

This experiment was pre-registered on the Open Science Framework (https://osf.io/8p4tx/). The pre-registration was conducted after the pre-tests were completed but before the start of the test.

Analysis

I conducted the same statistical analysis used by Legg and Clayton (2014). For each trial, I calculated the proportion of items cached in the *out-of-view* tray out of the total number of items cached in both trays. For the *Private* condition, these data were averaged across the two orientation trials. For the *Observed* condition, data were averaged across the two orientation trials and across the *Observed by dominant* and the *Observed by subordinate* trials (i.e. the four trials in the *Observed* conditions). Thus, the *Observed by dominant* and the *Observed by subordinate* conditions were merged. The average proportion of the caches in the *out-of-view* tray was then compared between the *Observed* and *Private* conditions using a one-tailed permutation test. Following Legg and Clayton (2014) I also tested whether the average number of items cached across both trays differed between the *Observed* and *Private* conditions by using a two-tailed permutation test. Statistical analyses were performed in R (R.3.5) using the RStudio 1.1.447 wrapper (RStudio Team, 2018) and the package *coin* (Hothorn et al., 2006). Alpha level was set to 0.05.

If Eurasian jays can adjust their caching behaviour according to the visual perspective of a conspecific, then cachers should – as reported by Legg and Clayton

(2014) – cache proportionately more items in the *out-of-view* tray when being observed by another bird than when in private.

5.2.2 RESULTS AND DISCUSSION

All birds in Colony 1, but only one bird of Colony 2 (Hunter) met the criterion of the Pre-test. Therefore, nine birds in total proceeded to the test.

After Dublin had received the first trial in the *Observed by dominant* condition, Rome – the individual acting as dominant observer for Dublin – appeared to experience problems with her wing and with flying. Out of welfare reason I therefore decided to exclude Rome from acting as the observer in Dublin's second trial in the *Observed by dominant* condition. Caracas, who was the highest ranked individual in the colony, was used instead. Because all other birds were tested with the same individual in the two *Observed by dominant* trials, I decided to re-do Dublin's first trial with Caracas. This ensured that the trials from which data for the Observed by dominant condition for Dublin were used for the analysis consistently had Caracas as the observer.

The jays cached a median of 1.82 item per trial (IQR = 2.50). The *Private* and *Observed* conditions did not differ in the number of items cached per trial (n=9, Z=-0.79, p=0.43; Fig. 5.2). Dublin and Lisbon consistently did not cache in any of the *Private* and *Observed* trials. Consequently, these two birds were excluded from further analyses because, given their performance, it was not possible to compare the proportion of items cached in the *out-of-view* tray between conditions. The remaining seven birds did not cache a higher proportion of items in the *out-of-view* tray in the *Observed* condition than in the *Private* condition (n=7, Z=-0.13, $p_{\text{one-tailed}}$=0.55; Fig. 5.3).

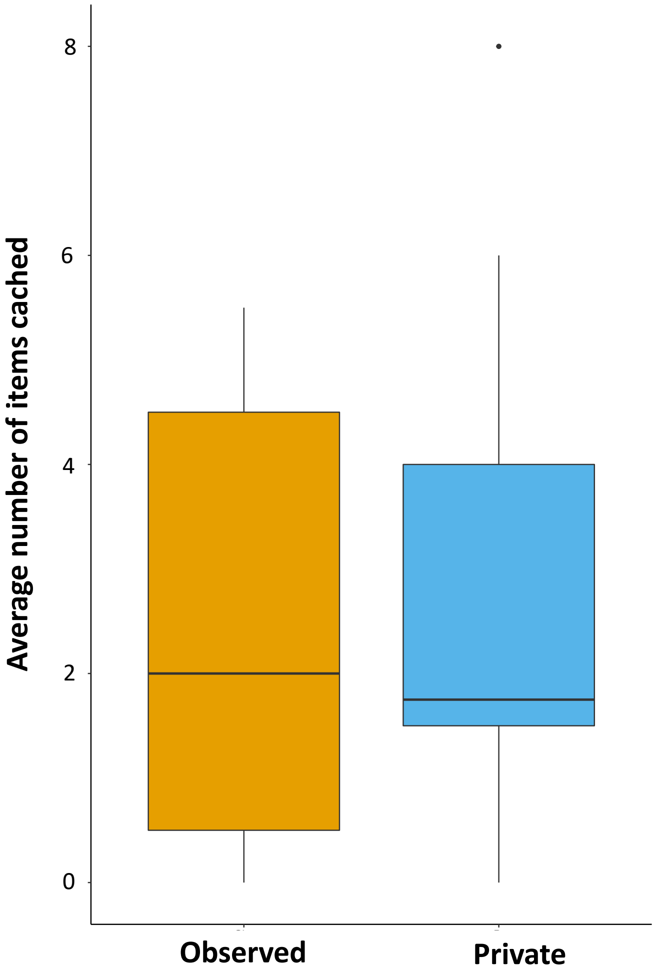

Figure 5.2: Box and whisker plot of data in Experiment 5.1. The plot shows the average number of items cached (in both trays) *Private* and *Observed* conditions. Note that data in the *Observed by dominant* and *Observed by subordinate* conditions were averaged.

These results are only to some extent compatible with those reported by Legg and Clayton (2014). In line with the original study, I found that jays cached a comparable amount of items (across both trays), when they were observed by a conspecific and when they were in private. Further jays in Legg and Clayton (2014)'s experiment cached a median of 2.5 items, a result seemingly comparable to the performance of the jays in this experiment. Crucially however, the original study reported that jays cached proportionately more items in the *out-of-view* tray when a conspecific was present than when in private. I could not find equivalent evidence in this experiment, thereby supporting the results of Experiment 4.1 (Chapter 4). Hence, Experiment 5.1 failed to replicate the effect reported by Legg and Clayton (2014), thereby possibly challenging the idea that Eurasian jays adjust their caching strategy by responding to the visual perspective of a conspecific.

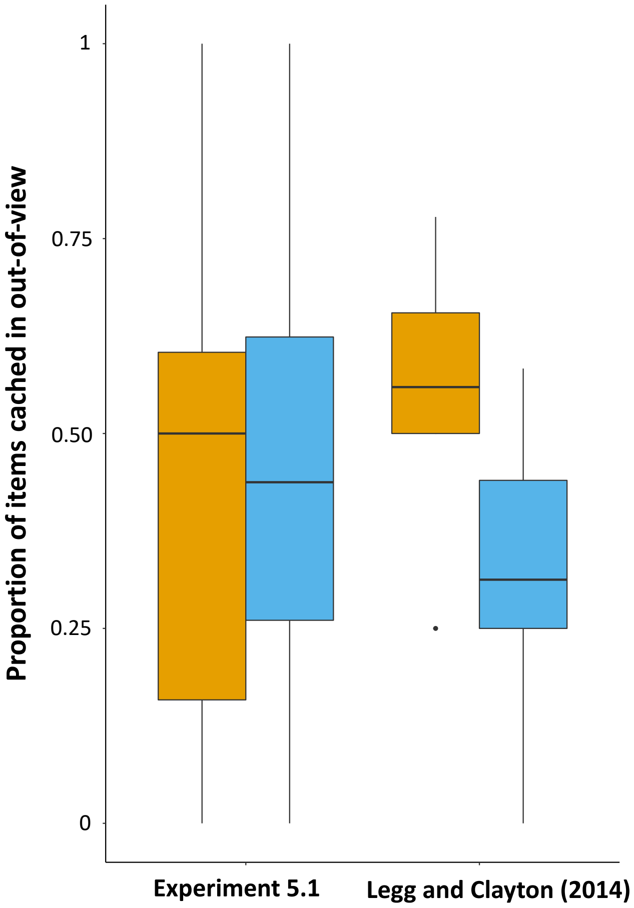

Figure 5.3: Box and whisker plot of data in Experiment 5.1 (left) and in Legg and Clayton (2014; right). The plot shows the proportion of items cached in the *out-of-view* tray out of the total number of items cached, in the *Private* and *Observed* conditions. Note that data in the *Observed by dominant* and *Observed by subordinate* conditions were averaged.

5.3: EXPERIMENT 5.2

The results reported in Chapter 4 were not only at odds with Legg and Clayton (2014)'s experiment but also with the study by Ostojić et al. (2017). In Experiment 5.2, I explored whether a minor difference in the set-up, i.e. presence or absence of a transparent barrier, may have caused the inconsistency in the results between Experiment 4.2 and Ostojić et al. (2017)'s study. To this end, I employed the same experimental set-up and procedures used in Experiment 4.2, except that here jays were presented either with the transparent U-barrier (*Barrier* condition) or with no barrier (*No-barrier* condition).

Thus, in contrast to Experiment 4.2 – where observer jays could either see the caching tray (*In-view* condition) or not see the caching tray (*Out-of-view* condition) – here observer jays had visual access to the caching tray in all conditions.

5.3.1 METHODS

Subjects

All eight birds in Colony 1 (as reported in Experiment 5.1; see also Appendix A) were tested. Six birds had participated in the test in Experiment 4.2. (Chapter 4). In contrast, of the remaining two birds, Lisbon took part only in the Familiarization but not in the test, while Dublin did not participate in any experimental phase in Experiment 4.2. In addition, five birds that were tested here (Caracas, Dublin, Rome, Quito and Washington) had also participated in the caching experiment conducted by Ostojić et al. (2017). All procedures were approved by the University of Cambridge Ethics Review Committee. The experiment was conducted in November 2018.

Experimental set-up

Birds were tested in indoor testing compartments (2x1x3 m) that were accessible from the aviary through flap windows. In the Familiarization birds was tested in private, i.e. with no other bird present in the test room. Testing compartments used during the Familiarization were not used in the test phase. In the test, a cacher bird and an observer bird were housed in adjacent compartments that were separated by opaque sheeting except for a mesh window (30x55 cm) through which the birds had visual access to the adjacent compartment.

The compartment contained a suspended platform (1x1 m) approximately 1 m from the ground, where caching trays, food bowls, and Perspex barriers could be placed. Rectangular seedling trays (5 x 3 pots filled with sand) were used as caching trays. Trays were painted different colours and were trial-specific to minimise the probability that birds' caching behaviour in one trial would be influenced by its memory from previous trials. The bowls contained i) a handful of maintenance diet (MD); ii) 50 Macadamia nut halves (M), or; iii) 50 whole peanuts with skin (P). Each type of food was presented in a bowl of a specific colour, and these colours were kept consistent for all birds.

The same transparent U-barrier as in Experiment 4.2 was used. This barrier consisted of two lateral Perspex sheets (26 x 25 cm) and one central Perspex sheet (53 x 25 cm) forming two angles of approximately 45°.

General Procedure

Approximately 1.5h prior to the start of Familiarization and test trials, the birds' maintenance diet was removed from the aviary to ensure that the birds were mildly hungry and thus likely to interact with food provided during testing. Test trials involved a pre-feeding phase followed by a caching phase. Before the start of the trial, two birds (one cacher and one observer) were given access to two adjacent compartments. Subsequently, I placed a bowl containing pre-feeding food (Macadamia nuts or peanuts) on the suspended platform in the observer's compartment and a bowl containing a handful of maintenance diet on the platform in the cacher's compartment. The bowls were placed in front of the mesh window (Fig. 5.4) to ensure that the birds could see each other whilst eating and to maximise the chances that the cacher could see on which food the observer was pre-fed. I then left the test room and the birds could eat the pre-feeding food for 15 minutes. Next, I entered the test room again and removed the bowls as well as any food remains on the platforms. In the subsequent caching phase, I positioned the caching tray, two food bowls, as well as the barrier (if required), in front of the mesh window in the cacher's compartment (Fig. 5.4). One bowl contained 50 Macadamia nut halves, while the other bowl contained 50 whole peanuts. I then left the test room and the birds were given 15 minutes, during which the cacher could eat and cache the foods in the tray. At the end of the trial, I opened the flap windows to allow the birds to re-join the rest of the group in the aviary and recorded the amount of food eaten and the number and location of caches in the tray. Approximately three hours after each trial, the cacher was allowed to re-enter the caching compartment. At this stage, the flap window was kept open so that the bird had access not only to the indoor compartment but also to the adjacent outside run. Note that the door connecting the outside run to the aviary was kept closed, thus no other bird could enter the cacher's run or compartment. The cacher could retrieve the hidden items and re-cache them in the compartment and in the adjacent small outdoor run for 10 minutes. Observers were not present during retrieval. This retrieval phase was conducted only to reduce the probability that birds would stop caching in the trays so that these data were not analysed. Birds received a single test trial per day.

Familiarization

Familiarization trials were conducted to ensure that birds were motivated to cache both types of food and were comfortable caching in a tray both when it was positioned close to the U-barrier and when no barrier was present. Birds received two trials on separate days. On each trial, birds were presented with a single caching tray and two food bowls, which were presented sequentially. Birds were given the opportunity to eat and cache for 20 minutes: during the first 10 minutes they were provided with one type of food and during the next 10 minutes with the other. The order in which the birds experienced the two types of foods was counterbalanced across birds and across trials, such that each bird experienced one order on their first trial and the opposite order on their second trial. In one trial, the transparent U-barrier was positioned close to the caching tray, whereas in the other trial no barrier was present. The order in which the birds received the two trials (i.e. with or without the barrier) was counterbalanced across birds. The compartments used in the Familiarization were not used in the subsequent test. To proceed to testing, birds had to i) cache at least one item on each trial (i.e. both with barrier present and with no barrier present), and ii) cache at least one item of each type of food across the two trials. If no item was cached in a trial, then that trial was repeated for a maximum of three times. Thus, a bird could receive a maximum of six trials in total. The repeated trials were conducted at the end: for example, if a bird's first trial had to be repeated, then this bird received the second, pre-planned trial on day 2, and subsequently it received the first trial again on day 3.

Test

Following the procedure of Experiment 4.2, in the pre-feeding phase cachers were first able to see an observer feeding on one specific type of food (Macadamia nuts or peanuts). In the subsequent caching phase, cachers were provided with a single tray and with two food bowls, one containing 50 Macadamia nut halves and one containing 50 whole peanuts with skin. All birds were tested in two conditions that differed in whether the transparent barrier was present or absent. In the *Barrier* condition, the caching tray was positioned within the transparent U-barrier, whereas in the *No-barrier* condition, no barrier was placed in the caching compartment (Fig. 5.4). Crucially, the observer bird had visual access to the caching tray in both conditions.

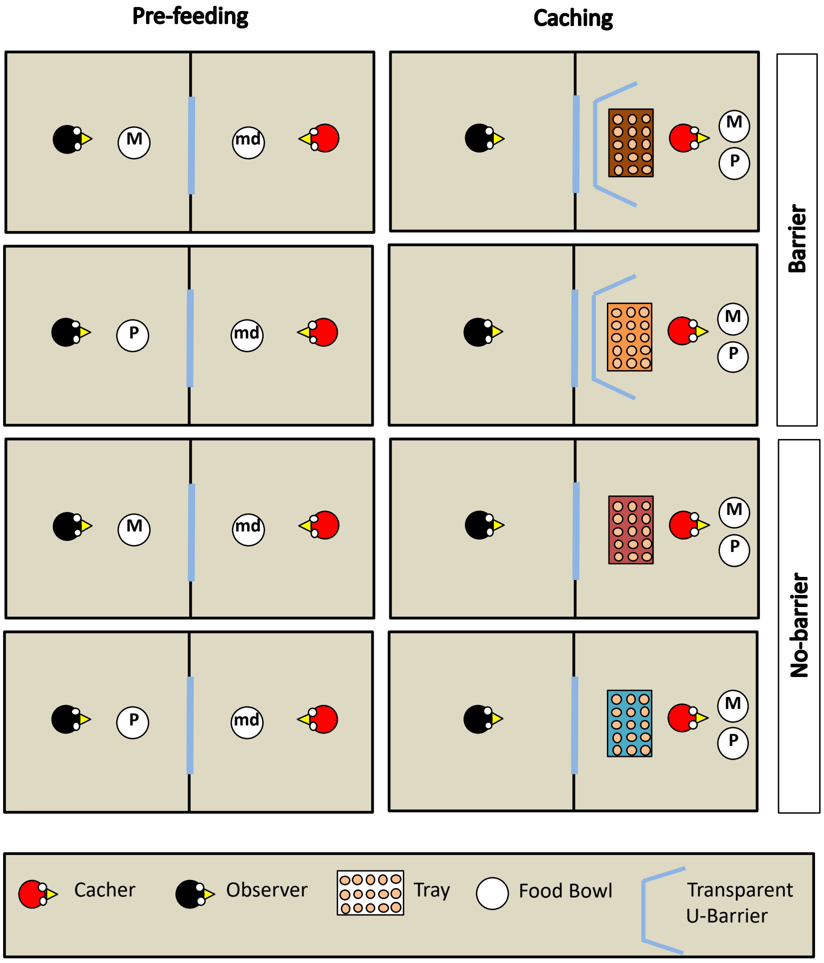

Figure 5.4: Top-view schematic representation of the set-up and procedure used in the test of Experiment 5.2. Trials were composed by a pre-feeding phase (left panels) and a caching phase (right panels). The cacher bird received two trials with the transparent U-barrier (*Barrier* condition, top panels), and two trials with no barrier (*No-barrier* condition, bottom panels). Within each condition, trials differed in the type of food (either peanuts, P, or Macadamia nuts, M) that was provided to the observer in the pre-feeding phase. The cacher bird was always presented with a handful of maintenance diet (md) in the pre-feeding phase of all trials.

In each condition, the birds received two trials: one in which the observer was pre-fed on one type of food (e.g. Macadamia nuts) and one in which the observer was pre-fed the other type food (e.g. peanuts). Birds first received both trials of one condition (e.g. *Barrier* condition), and then the two trials of the other condition. The order in which the two conditions were conducted was counterbalanced across birds. The order in which observers were pre-fed the two kinds of food within a condition was counterbalanced across birds, but kept consistent across conditions such that the order of the two trials for each bird was the same in both conditions. If a bird did not cache any items in one or two trials, those trials were repeated at the end of the experiment. Each trial could be repeated no more than two times. If a bird cached no item in more than two trials, that bird was not tested any further and was excluded from the analysis.

This experiment was pre-registered on the Open Science Framework (https://osf.io/8p4tx/).

Analysis

The statistical approach that was originally planned (as described in the Pre-registration, OSF) involved the transformation of raw data (i.e. the number of peanuts and Macadamia nuts cached) into proportions of items cached in the *out-of-view* tray out of number of items cached in both trays. I subsequently opted to use a slightly different approach, namely to transform raw data into difference scores (for example, number of items cached in *out-of-view* tray minus number of items cached in *in-view* tray). This was done to be more consistent within the thesis and thus to facilitate the comparison with Experiment 4.2, in which difference scores were used to analyse the data. Note however, that the two approaches yielded the same results. In what follows, I provide the details of the statistical approach that was used.

For each individual, I calculated the difference in the number of peanuts cached minus the number of Macadamia nuts cached. This difference score – $[P_{\text{cached}} – M_{\text{cached}}]$ – represents an indication of a preference to cache P over M. I tested whether – within the *Barrier* and the *No-barrier* conditions – the difference score was greater when observers were sated on P than when they were sated on M, using a one tailed Wilcoxon signed-rank test. I further calculated a difference of difference scores, namely in each condition, I subtracted the difference score of the trial in which the was observer pre-fed M from the difference score of the trial in which the observer was pre-fed P: $[P_{\text{cached}} – M_{\text{cached}}]_{\text{pre-fed P}} – [P_{\text{cached}} – M_{\text{cached}}]_{\text{pre-fed M}}$. This difference of difference scores represents an indication of a preference to cache P over M when the observer was sated on P relative to when the observer was sated on M. This variable was compared between conditions using a Wilcoxon signed-rank test. Statistical analyses were performed in R (R.3.5) using the RStudio 1.1.447 wrapper (RStudio Team, 2018). Alpha was set to 0.5.

If Eurasian jays can adjust their caching behaviour according to the current desire of a conspecific, then cachers should – in both conditions – cache preferentially P when the observers were sated on P than when they were sated on M. If this caching strategy is not affected by the presence of a transparent barrier, then the difference of difference score should not differ between the *Barrier* and the *No-barrier* conditions.

5.3.2 RESULTS AND DISCUSSION

All birds passed the Pre-test and therefore proceeded to the test. One bird (Lisbon) consistently cached no items in the first three test trials and was thus excluded from further testing. Thus, a total of seven birds completed the test.

In both conditions, the difference score – [P_{cached} – M_{cached}] – was not greater when the observer was sated on peanuts than when it was sated on Macadamia nuts (Wilcoxon Signed Rank Test: *Barrier* condition, n=7, W=1, $p_{\text{one-tail}}$=0.50; *No-barrier* condition: n=7, W=-9, $p_{\text{one-tail}}$=0.91; Fig. 5.5). Thus birds did not preferentially cache the food that was less desired by the observer, regardless of whether the transparent barrier was present or absent.

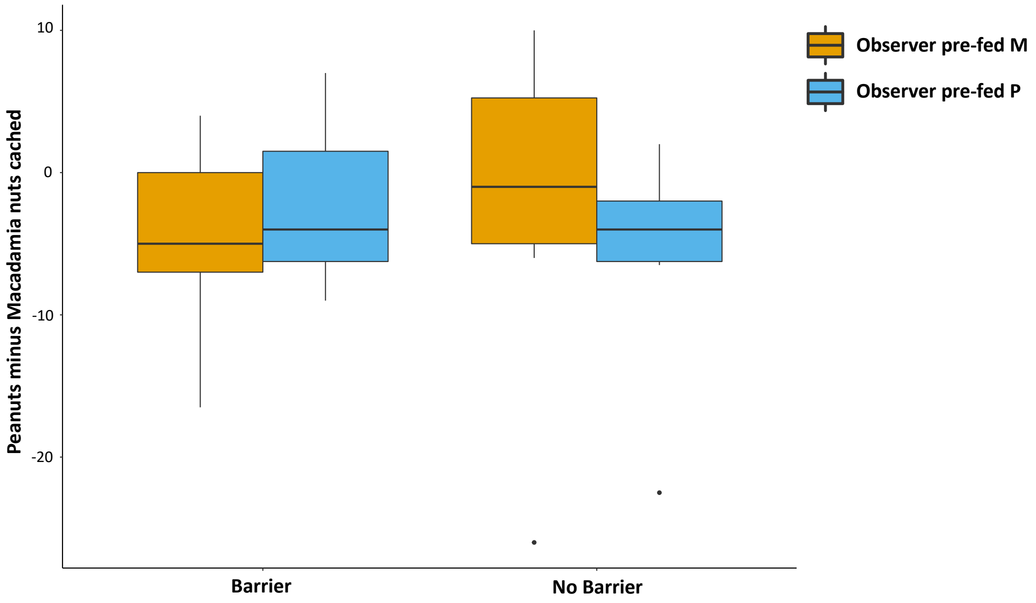

Figure 5.5: Box and whisker plot of data in Experiment 5.2. The plot shows the difference in the number of peanuts cached minus the number of Macadamia nuts cached in the *Barrier* condition (left) and *No-barrier* condition (right). The colour of the boxes in the plot differs on the basis of the type of food that was provided to the observer in the pre-feeding phase: blue denotes that the observer had been pre-fed P and orange denotes that the observer had been pre-fed M.

Supporting this result, the difference of difference score – $[P_{\text{cached}} - M_{\text{cached}}]_{\text{pre-fed P}} - [P_{\text{cached}} - M_{\text{cached}}]_{\text{pre-fed M}}$ – was comparable between conditions (Wilcoxon Signed Rank Test: n=7, W=15, p=0.14). Therefore, the presence or absence of the barrier had no significant effect on the caching behaviour.

Taken together, these results appear to corroborate the findings of Experiment 4.2 and in parallel, question the robustness of the effect reported by Ostojić et al. (2017) and the claim that Eurasian jays take into account the current desire of a conspecific to most effectively protect their caches.

5.4: GENERAL DISCUSSION

In this chapter, I explored the robustness of two established caching strategies in Eurasian jays. In Experiment 5.1, I conducted a replication of Legg and Clayton (2014)'s study in which it was reported that, when observed by a conspecific, Eurasian jays protect their caches by hiding a larger proportions of items behind opaque barriers than when they are alone. My results could not support the findings of the original study: I found that jays did not cache proportionately more in the out-of-view location when a conspecific was present than when in private. In Experiment 5.2, I tested whether jays' ability to adjust their caching behaviour according to the current desire of a conspecific – as reported by Ostojić et al. (2017) – is affected by the presence of a transparent barrier positioned in proximity of the caching location. I decided to investigate this issue with the aim of clarifying the results of Experiment 4.2. Results Experiment 5.2 showed that jays' caching pattern did not differ between when the barrier was present and when it was absent. Crucially however, results were not in line with Ostojić et al. (2017)'s evidence: I found that jays exhibited no preference for caching more items of the same type food that the observer jay had been sated on over an alternative food that was not eaten by the observer.

From a theoretical perspective, two alternative explanations can account for the inconsistent results between Experiment 5.1 and Legg and Clayton (2014)'s study. First, if Eurasian jays are actually capable of caching according to the visual perspective of another bird, then the replication represents a false negative. Second, if jays are not endowed with this capability, then the original study was a false positive. Based on this evidence alone, it is not possible to draw firm conclusions on which of the two explanations should be given more credit, also because the small sample size (Experiment 5.1, n=7; Legg and Clayton (2014), n= 6) may have fostered the chance of false positive in the original study, and limited the power of the replication (Farrar and Clayton, 2019). However, some considerations can be made. On the one hand, the possibility that the effect reported in the original study is a true effect would fit with the current corvid literature. Shaw and Clayton (2013) found that Eurasian jays prefer to cache in non-noisy substrates when with a conspecific that could hear but not see them caching, thus raising the possibility that these jays may take into account the acoustic perspective of competitors to protect their caches. Further, a number of experiments indicated that fellow corvids employed cache protection strategies based on the visual perspective of conspecifics. For instance, in the presence of a conspecific California scrub-jays seems to cache preferentially in shadow or out-of-view locations (Dally et al., 2004, 2005), and both California scrub-jays and ravens appear to cache further away from competitors (Dally et al., 2005; Heinrich and Pepper, 1998) and protect their caches if a non-visible conspecific had the opportunity to witness the caching event but not if the conspecific could not have seen it (Bugnyar et al., 2016; Dally et al., 2006). Yet, as discussed in the introductory chapter of this thesis, it is problematic to assume that a given cognitive ability is widespread within a taxon based on sporadic reports in a few species. On the other hand, the possibility that the replication I have conducted yielded a false negative outcome seems particularly hard to reconcile with the results of Chapter 4. Consistently with Experiment 5.1, jays did not prefer to cache behind an opaque barrier (over caching behind a transparent barrier) in Experiment 4.1. Additionally, comparable results also emerged from an exploratory study employing a procedure very similar to that of the original study but involving a lower number of trials, i.e. Eurasian jays (n=7) received only one trial in the *Private* condition and one trial in the *Observed* condition (Ostojić, unpublished data[10]).

In principle, these lines of reasoning are also applicable to the comparison between the results of Experiment 5.2 and those reported by Ostojić et al. (2017). On the one hand, if Eurasian jays can adjust their caching behaviour by taking into account the current desire of a competitor, then the findings of Experiment 5.2 are a false negative. Alternatively, if jays are not capable of this caching strategy, then Ostojić et al. (2017)'s result is a false positive. It is possible to raise the argument that Experiment 5.2 was not an exact replication of Ostojić et al. (2017)'s experiment, so that limited

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[10] Further details of the procedure and results can be found at https://osf.io/8p4tx/.

conclusions can be drawn. However, Experiment 5.2 – and, with a minor difference in set-up, Experiment 4.2 – faithfully replicated the *Seen* condition of Ostojić et al. (2017)'s experiment but consistently failed to reproduce the effect described in the original study. In addition, further support for the possibility that Eurasian jays might not adjust their caching pattern on the basis of a competitor's desires comes from another study. Crosby (2019) replicated both the *Seen* and *Unseen* conditions of Ostojić et al. (2017)'s experiment but could not corroborate the original results. Specifically, in both conditions, the author found that jays had no preference for caching the food that observer was motivated to pilfer over the alternative food. Interestingly, in the cooperative context of food sharing, the original finding by Ostojić et al. (2013) that male Eurasian jays choose which food to cater to their mate according to latter's desires was consistently replicated in follow-up studies (Ostojić et al., 2014, 2016). Therefore, caution should be taken in generalizing across contexts the reliability with which jays are capable of responding to others' desires.

In the light of these considerations, it is not possible to conclude that the caching strategies reported by Legg and Clayton (2014) and Ostojić et al. (2017) represent robust and reliable effects in Eurasian jays. It cannot be excluded that jays' inability to integrate others' perspective and current desire (as reported in Chapter 4) may have more simply resulted from their limited skills to respond to each social cue independently, rather than from their lack of ability to process different types of social cues simultaneously.

Finally, some thoughts should also be given to an alternative explanation for why I could not replicate previously reported caching strategies. The Eurasian jays that I tested in Chapter 5 (and Chapter 4) have participated in a number of caching experiments with similar set-ups (e.g. caching occurring when a conspecific is housed in an adjacent compartment) over the years. It is theoretically possible that the repeated exposure to similar experimental settings may have affected the jays' performance, thus impairing the replication of original effects in the subsequent studies. For instance, if the Eurasian jay can learn over trials/studies that all items that are cached are always given back at recovery (i.e. there is no actual pilfering risk), then the bird may progressively stop protecting the caches when observed by a conspecific. Given the potential wide-reaching implications of this issue on our understanding of cognition in the Eurasian jay (or perhaps in corvids), it would be particularly important for future studies to investigate the influence of an individual experimental history on his performance in subsequent tests.

The first objective of this thesis is to gain further insight into the process of convergent cognitive evolution between corvids and apes. To explore whether corvids, as apes, are endowed with a flexible and domain general cognitive tool-kit, Chapters 2 to 5 reported four empirical studies investigating problem solving, future planning and social abilities in the Eurasian jay. In Chapter 6 I turn my attention to the second objective of the thesis, namely to explore the potential of coleoid cephalopods as a novel model group for the study of convergent cognitive evolution.

CHAPTER 6[11]:

Cephalopods: a new model group for studying convergent cognitive evolution?

Abstract

In Chapters 2 to 5 I explored whether corvids are endowed with a flexible cognitive tool-kit by testing physical problem solving, future planning and social cognition in the Eurasian jay. In this chapter, I turn my attention to the second objective of this thesis, namely the aim to lay theoretical and methodological groundwork for the study of convergent cognitive evolution between cephalopods and large-brained vertebrates. To this end, I first review the most remarkable examples of behavioural flexibility in cephalopods and propose that current evidence may be sufficient to hypothesize a case of first-level convergence (Seed, 2007), i.e. convergence at the behavioural level, between these molluscs and large-brained vertebrates. Subsequently, I consider the evolutionary process(es) that may have triggered the emergence of large brains and flexible behaviour together with short life-history in cephalopods. I suggest that the disappearance of the protective shell may have (i) produced a dramatic increase in unavoidable mortality thus selecting fast life histories, and, in parallel (ii) facilitated widespread colonization of complex niches, thus driving cephalopods to cope with novel challenging problems. Cephalopods' cognitive sophistication might have emerged primarily in response to predation and complex feeding contexts but social challenges, particularly during mating, might have acted as additional selective pressures. Finally, I conclude by presenting a number of novel paradigms that could be used to investigate tool use, future planning and social cognition in the octopus, and thus to explore convergent cognitive evolution between cephalopods and large-brained vertebrates at a deeper level of analysis.

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[11] Part of this chapter has been published as: Amodio P., Boeckle M., Schnell A. K., Ostojić L., Fiorito G., & Clayton N. S. (2019). Grow Smart and Die Young: Why Did Cephalopods Evolve Intelligence?. *Trends in Ecology and Evolution*, 34(1), 45-56. doi.org/10.1016/j.tree.2018.10.010

6.1: INTRODUCTION

In the first part of this thesis (Chapters 2 to 5) I investigated the Eurasian jay's cognitive sophistication in different domains to explore Emery and Clayton (2004)'s hypothesis that corvids may have evolved – convergently with apes – a flexible and domain general cognitive tool-kit. In this chapter I continue my study of convergent cognitive evolution by turning my attention to the second objective of this thesis and by focusing on another model group, namely the cephalopods. Here, I will lay theoretical and methodological groundwork for studying convergent cognitive evolution between cephalopods and large-brained vertebrates.

As discussed in Chapter 1, indicators of complex cognition such as large brain and behavioural flexibility have been reported in distantly related lineages, most notably primate, cetaceans, elephants, corvids, and parrots (Emery and Clayton, 2004; Fox et al., 2017; Plotnik and Clayton, 2015). Differences in evolutionary history and brain structure among these taxa suggest that i) complex cognition may have emerged multiple times independently (Roth, 2015); and ii) distinct neural substrates, such as the avian nidopallium and the mammalian cortex, can support equivalent cognitive sophistication (Güntürkün and Bugnyar, 2016). Despite their differences in evolutionary history and neural substrates, primates, cetaceans, elephants, corvids, and parrots appear to share comparable socio-ecological challenges and slow life histories. Thus large-brained vertebrates may have evolved enhanced cognition convergently, in response to similar selective pressures, namely the need to navigate complex social environments and to find and process food (Emery and Clayton, 2004; Fox et al., 2017; Plotnik and Clayton, 2015). Further, the positive correlation between brain size and the long developmental trajectory reported in mammals and birds (Gonzales-Lagos et al., 2010; Minias and Podlaszczuk, 2017; Street et al., 2017; Wirthlin et al., 2018) suggests a co-evolutionary scenario for the evolution of these traits: the slow life history might have been necessary to overcome the costs of a large brain and/or a consequence of the reduced extrinsic mortality resulting from enhanced intelligence (Barton and Capellini, 2011; Sol, 2009a)

This convergent evolutionary route, however, cannot explain why large brains and complex behaviours emerged in cephalopods (Fig. 6.1). Coleoid cephalopods (cuttlefish, squid, and octopuses) are shell-less molluscs that are considered to be the most cognitively advanced group of invertebrates. They evolved a unique mixture of convergent and divergent features relative to the main groups of intelligent vertebrates

(Tab. 1). On the one hand, cephalopods are endowed with a sophisticated nervous system, which both resembles that of vertebrates in relative size (Packard, 1972) and complexity (Hochner et al., 2006; Young, 1991) and supports strikingly flexible behavioural repertoires (Darmaillacq et al., 2014; Hanlon and Messenger, 2018; Marini et al., 2017; Mather and Dickel, 2017). On the other hand, cephalopods do not appear to engage in complex social bonds (Boal, 1996; Schnell and Clayton, 2019) and have fast life histories with typical lifespans shorter than two years, no parental care, and in some cases, terminal reproduction (Rocha et al., 2001).

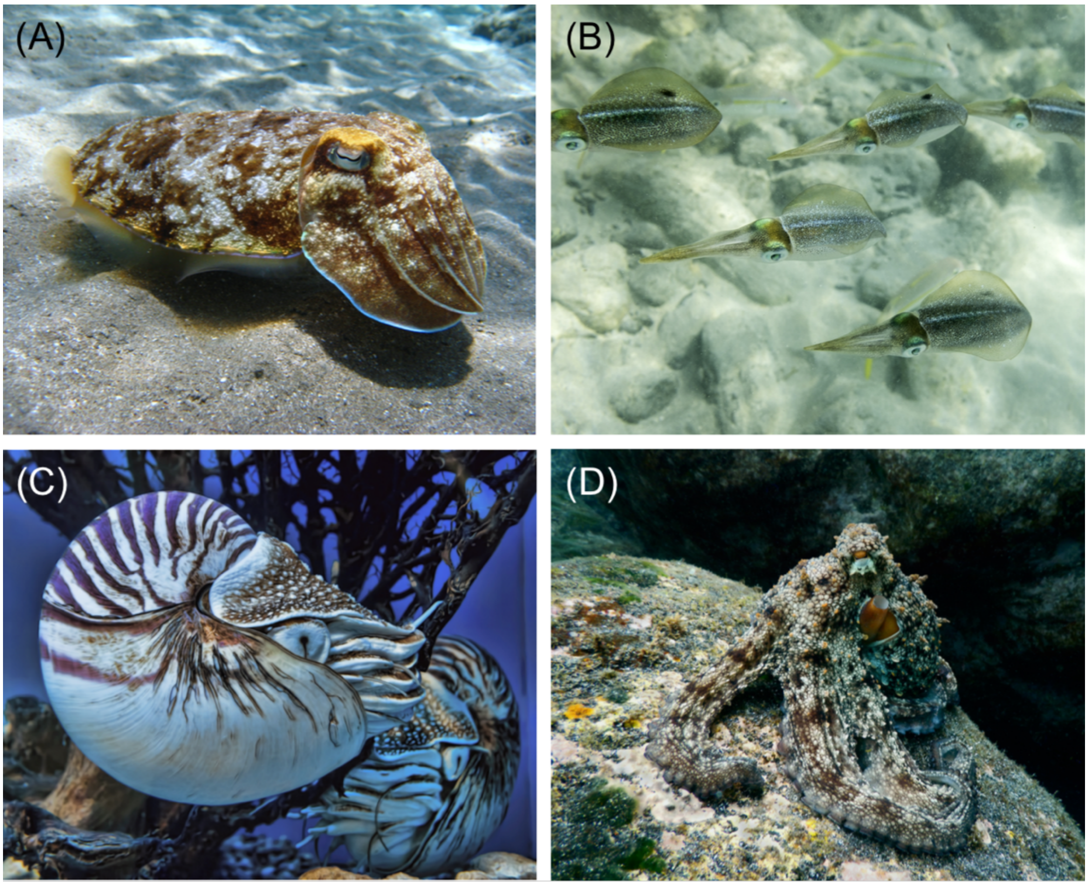

Figure 6.1: Cephalopods. (A) Cuttlefish, *Sepia officinalis* (credit egiverga, stock.adobe.com), (B) Caribbean reef squids, *Sepioteuthis sepioidea* (credit kirk, stock.adobe.com), (C) Nautilus, *Nautilus pompilius* (credit carljf, stock.adobe.com), (D) Common octopus, *Octopus vulgaris*.

In what follows, I first review current evidence of cognitive sophistication in cephalopods and discuss the level at which they may have converged with cognitively advanced groups of vertebrates. Subsequently, I consider the factors selecting for large brain, complex behaviour together with fast life histories in cephalopods, highlighting the convergent and divergent aspects between these molluscs and large-brained vertebrates. Finally, I propose novel paradigms that may allow researchers to gain a deeper understanding of convergent cognitive evolution in cephalopods by measuring cognitive sophistication in the common octopus, an iconic model species for the study of behaviour and cognition in cephalopods.

Table 6.1: Convergent and divergent features between cephalopods and large-brained vertebrates. The colours of the cells refer to traits that are highly variable across the groups (blue), or shared (green) or not shared (orange) between the cephalopods and the groups of vertebrates

	Trait	Cephalopods	Corvids	Cetaceans	Apes
Morphology	Manipulative Appendages	Suckered arms and tentacles	Beak and Feet	Rostrum	Hands
	Dexterity	High	High	Limited	High
Senses	Vision	High	High	High	High
	Acustic	Limited	High	High	High
	Smell Chemotactic	High	Limited	Limited	Limited
Brain	Brain-Body Size Ratio	High	High	High	High
	Substrate for Complex Cognition	Vertical lobe	Nidopallium	Cortex	Cortex
Ecology	Life Style	Aquatic	Flight	Aquatic	Terrestrial/Arboreal
	Diet	Carnivores	Generalistic	Carnivores	Generalistic
	Extractive Foraging	Present	Present	Absent	Present
	Predation	High	Limited	Limited	Limited
Social Life	System	Solitary/Anonymous schools	Pairs/Groups	Family Groups	Groups
	Long-term Bonds	Absent	pair mate	multiple individuals	multiple individuals
Behavioral Flexibility	Find and Process Food	High	High	High	High
	Social Interactions	Limited?	High	High	High
	Predator Avoidance	High	?	?	?
Life History	Life Span	0.5-2 years	> 15 years	> 40 years	> 40 years
	Parental Care of Offspring	Absent	Present	Present	Present
	Reproduction	Semelparous strategies	Iteroparity	Iteroparity	Iteroparity

6.2: HOW COMPLEX IS CEPHALOPODS' COGNITION?

As discussed in Chapter 1, cognitive sophistication cannot be measured directly and is thus typically estimated through morphological and behavioural proxies, namely brain features and behavioural flexibility. Although cephalopods' brains differ from those of vertebrates in many aspects, they are similar in relative size and complexity to those of vertebrates that are considered intelligent. Further, there appears to be considerable convergence in behavioural complexity between cephalopods and large-brained vertebrates.

6.2.1 Nervous system

Cephalopods have a remarkably large nervous system (up to 500 million neuronal cells in the octopus) that comprises a unique mixture of classic molluscan features and more complex vertebrate-like traits (Shigeno et al., 2018). The brain is formed by the aggregation of several ganglia (i.e. lobes) that show the typical neuronal arrangement of invertebrates, with cell bodies surrounding internal layers of synaptic connections (Young, 1971). However, the relative size of the cephalopods' brain (Packard, 1972) and the high density of inter-neurons resemble that of some vertebrates (Shomrat et al., 2015; Young, 1991, 1995).

The number and function of the lobes differ substantially across cephalopods, depending on species-specific lifestyles (Nixon and Young, 2003). Among the various lobes that constitute the cephalopod brain, the vertical lobe plays a pivotal role in learning and memory in all coleoids (Fiorito and Chichery, 1995; Grasso and Basil, 2009) and has been compared to regions of the mammalian cortex and the avian nidopallium (Edelman and Seth, 2009; Young, 1995). In contrast to birds and mammals, the processing of motor and sensory inputs in cephalopods is only partially dependent on the central brain. The optic lobes, a pair of large nervous structures located outside the cartilaginous capsule of the brain and connected to the retinae of the lens eyes, are essential for the computation of visual input (Young, 1995). Furthermore, the processing of chemo-tactile information and motor programmes is performed through the concerted action of higher centres (i.e. the inferior frontal lobe system; Young, 1991, 1995) and the nervous system of the arms. In the octopus, the peripheral neural components encompass up to 60% of the total number of cells and embed the neural information for the execution of basic movements of the arms (Hochner, 2012) in a stereotyped autonomous way (Sumbre et al., 2005). Thus, the nervous system of cephalopods represents a striking example of embodied organization in which the central brain acts as a decision-making unit that integrates multi-modal sensory information and coordinates the motor commands executed by the periphery. These idiosyncratic features of the nervous system as well as the suggested lack of somatotopic organization of the central brain (Zullo et al., 2009; but see Marini et al., 2017; Shigeno et al., 2018) might have evolved to allow cephalopods to cope with the computational constraints associated with their body plan and physiology (for instance, the need to coordinate the movement of eight arms and hundreds of suckers in the lack of a skeletal support; Hochner, 2012; Shigeno et al., 2018).

6.2.2: Behaviour

Problem solving and tool use

Problem solving and flexible tool use are considered hallmarks of physical intelligence (Byrne, 1997). Cephalopods, particularly octopuses, show considerable skills in these tasks. In the wild, octopuses express high flexibility in solving demanding problems, such as feeding on bivalves. According to the size and species of the prey, these animals can use their suckered arms to pull open the valves or drill holes through the shell to inject paralyzing toxins into the prey (Fiorito and Gherardi, 1999). These extractive foraging techniques are thought to improve with experience. For example, adult octopuses prey more efficiently on bivalves than juveniles by optimizing the site and number or holes drilled in the shell (reviewed in Marini et al., 2017). Therefore, like in tool use in corvids (Kenward et al., 2006), learning can play a key role in octopus problem solving by allowing the fine-tuning of innate predispositions.

Critically, octopuses exhibit flexibility not only when solving problems in their natural environment, but also when faced with artificial tasks. For instance, common octopuses remove lids from jars and open opaque boxes to acquire hidden prey (Amodio and Fiorito, 2013; Fiorito et al., 1990), as well as retrieve L-shaped food containers from crevices with or without visual access to the container and regardless of the spatial orientation of the container (Richter et al., 2016). The performances of the octopuses in these experiments were incompatible with simple learning mechanisms (e.g. trial-and-error learning; Fiorito et al., 1990; Richter et al., 2016), supporting the idea that problem solving might entail more complex cognitive underpinnings.

Just like some species of apes, cetaceans, and corvids, some cephalopod species are tool users. These animals squirt water jets from their funnels (using water as a tool) for a variety of purposes, such as to distance scavenger fishes, aid burrowing or remove food remains (Mann and Patterson, 2013). These behaviours may not represent stereotyped actions triggered by undesired stimuli because they are also performed during interactions with floating objects that have been classified as play (Kuba et al., 2003; Mather and Anderson, 1999). In addition to water, octopuses also use solid objects as tools. Several octopus species use stones to block the entrance of their dens (Mather, 1994, 2016). Furthermore, veined octopuses (*Amphioctopus marginatus*) assemble pairs of coconut shells into mobile dens and carry them around for future use (Finn et al., 2009). This rare example of composite tool use in invertebrates might – potentially –

be underpinned by cognitive sophistication for two reasons. First, this tool use might represent a behavioural innovation allowing octopuses to protect themselves from predator attacks in habitats where rocky shelters are scarce. Second, because coconut shells are transported to meet apparent future needs and despite considerable costs (e.g. conspicuous locomotion), this behaviour might rely on planning capabilities (Finn et al., 2009). However, future controlled experiments are required to exclude lower-level explanations. For instance, octopuses may carry around coconut shells only because these objects have previously become associated with a positive outcome, such as a thwarted attack by a predator or reduced stress from being covered by a protective casing.

Anti-predatory behaviours

The camouflage abilities of cephalopods are perhaps the most iconic evidence of their behavioural flexibility. Through the neuromuscular control of peculiar skin organs (e.g. chromatophores), these animals can alter their body patterns almost instantaneously to deceive predators (Borrelli et al., 2006; Messenger, 2001). By changing the colour and the texture of their skin, cephalopods can mimic dangerous heterospecifics (e.g. sea snakes; Norman et al., 2001) and achieve different kinds of camouflage (e.g. crypsis, countershading, masquerade; Hanlon and Messenger, 2018). Cephalopods adjust their anti-predatory strategies not only to the features of the substrate (Hanlon, 2007; Josef et al., 2012, 2015) but also to the type of threat. For instance, young cuttlefish (*Sepia officinalis*) express false eyespots towards visual predators but perform immediate flee responses towards chemosensory predators (Langridge et al., 2007). Similarly, cuttlefish and squid conceal themselves on the substrate when approached by pelagic fishes but flee away from the bottom when ambush predators are detected (Staudinger et al., 2011, 2013a). The recent discovery that cephalopods can change their appearance (e.g. break camouflage) to receive food rewards (Hough et al., 2016) suggests that these anti-predatory responses are not entirely hard-wired but instead entail learning and complex decision-making.

Future research might uncover further anti-predatory strategies that are candidates for complex cognition. The BBC Blue Planet II series recently showed a common octopus using his suckered arms to create spherical armour of stones and shells against hunting sharks (Jeffs and Brownlow, 2017). This behaviour is functionally similar to the use of coconut shells as a tool by the veined octopuses and might provide further insight into the flexibility of their anti-predatory behaviours.

Social behaviour

Although cephalopods primarily evolved dynamic skin as an anti-predatory weapon (Packard, 1972), their ability to rapidly alter their appearance is also used to communicate visually with conspecifics (Hanlon and Messenger, 2018; Lin et al., 2017; Moynihan, 1985). This sophisticated communication system allows cephalopods to convey honest and deceptive signals simultaneously. By longitudinally splitting the body into two parts, small male cuttlefish can express courtship displays towards a receptive female on one side of their body and deceptive female colourations towards a rival male on the other side of their body (Brown et al., 2012). Male mourning cuttlefish (*Sepia plangon*) have been reported to use this strategy only in front of one female and a single rival male, perhaps because the effectiveness of the female mimicry will be impaired in the presence of multiple males (Brown et al., 2012). In a similar vein, male giant cuttlefish (*Sepia apama*) adjust their fighting strategy in response to the size and fighting ability of their competitor (Schnell et al., 2015). Comparable levels of flexibility in a mating context are also observed among squids (Marian et al., 2019) and octopuses. In algae octopuses (*Abdopus aculeatus*), males adjust their mating tactics to their chances of winning agonistic encounters. Specifically, males avoid mate guarding if larger rivals are around to minimise the risk of fights and of being cannibalized (Huffard et al., 2010).

Cephalopods' behavioural flexibility in social contexts might extend beyond competitive interactions with conspecifics. Preliminary observations indicate that reef octopuses (*Octopus cyanea*) associate with hunting groupers in the Australian Great Barrier Reef (Unsworth and Cullen-Unsworth, 2012; Vail et al., 2013). In addition, groupers employ the same visual signal to communicate the location of hidden prey to their usual hunting partners, moray eels, and to octopuses (Vail et al., 2013).

On a superficial level, these interspecific interactions might look like cooperative hunting based on the complementary skills of the two species: speed for chasing prey in open water by the grouper and capability of reaching prey hidden in narrow crevices by the octopus. Critically, however, no predation by an octopus has been observed in this context, thus this interpretation remains speculative. Nevertheless, these observations indicate that hunting might provide one useful context within which to investigate cephalopods' flexibility in social interactions.

6.2.3: Level of convergence

Based on this evidence, can we consider cephalopods to have evolved complex cognition convergently with large-brained vertebrates? If this is the case, at what level of analysis did cognition evolve convergently in these groups? According to Mather (2019) cephalopods: '[…] can perform the operations suggested by Emery and Clayton (2004) as indicative of cognitive ability in mammals and birds — flexibility, causal reasoning, prospection, and imagination' (page 2; see also Mather and Dickel, 2017). Within the hierarchical framework proposed by Seed (2007), Mather's view corresponds to the third and deeper level of convergence: cephalopods and large-brained vertebrates independently evolved similar cognitive mechanisms underlying complex behaviours. In my view, this hypothesis is to date highly speculative. The current understating of cephalopods cognition is still very limited because the cognitive underpinnings of their behaviours have rarely been tested (but see Jozet-Alves et al., 2013; Yang and Chiao, 2016). Given that flexible behaviours can be supported by simple cognitive mechanisms (Mikhalevich et al., 2017; Seed et al., 2009a; Shettleworth, 2010), it is not possible to draw conclusions about whether cephalopods' behavioural flexibility is matched by equivalent cognitive complexity, as it appears to be the case in, for example, apes and corvids. For instance, Mather (2019) suggests that the *Passing Cloud* display (Packard and Sanders, 1971) and the avoidance of stinging anemones (Ross, 1971) provide evidence that cephalopods are capable of causal reasoning – the ability to identify the functional relationship between a cause and its effect. The *Passing Cloud* is a sophisticated skin display characterized by a well-defined dark area that seems to 'move' directionally on the animal's body (Packard and Sanders, 1971). Cephalopods most often exhibit this behaviour to startle prey, as well as conspecifics or other animals. While it is theoretically possible that the *Passing Cloud* could involve causal reasoning, this interpretation is premature without careful empirical testing (Amodio, 2019). It cannot be ruled out that *Passing Cloud* has a strong genetic component and/or it is the expression of simple learning mechanisms. Similar arguments can be raised in regard to the second putative behavioural evidence of causal reasoning. Ross (1971) reported that octopuses: i) progressively inhibit their predatory response selectively toward hermit crabs that had a stinging anemone attached to their shells, and ii) behave as if they have received a 'punishment stimulus' after touching an anemone. Therefore it seems possible that octopuses may develop avoidance of stinging anemones as a result of associative learning when physical interactions with the anemone have previously become associated with a negative outcome (Godfrey-Smith, 2019).

Despite the fact that a deep-level cognitive convergence between cephalopods and large-brained vertebrates is currently unwarranted, the richness and flexibility of cephalopods' behavioural repertoire is absolutely remarkable, not just among molluscs but in absolute terms. Thus – in my view – current evidence is sufficiently strong to support the hypothesis of *first-level* convergence between these groups: cephalopods and large-brained vertebrates may have converged behaviourally, i.e. they may have independently evolved behaviours that superficially appear comparably complex and flexible. Only through a careful testing of cephalopods' cognitive abilities in different domains will it be possible to explore convergence at the second level of analysis (Seed, 2007) and thus to evaluate whether cephalopods' behaviour is actually underpinned by cognitive mechanisms more complex than hardwired predisposition or simple learning processes.

6.3: CEPHALOPODS' ROUTE TO COGNITIVE SOPHISTICATION

If – as I have proposed – cephalopods' evolution can be taken as a case of first-level convergence with large-brained vertebrates, then it is necessary to consider why cephalopods – as short-lived invertebrates facing simple social environments – should have evolved large brain and behavioural flexibility, and thus potentially cognitive sophistication. The answer to this question is likely to be tightly linked to the dramatic changes in the shells that marked cephalopods' divergence from other molluscs.

Around 530 MYA a group of snail-like molluscs experienced a major shift in their morphology and physiology: their protective shell became a buoyancy device (Kröger et al., 2011; Tanner et al., 2017). The comparison with nautiluses, the only extant cephalopods who retained the external shell, suggests that this key event co-occurred with the emergence of arms, funnel, and crucially, a centralized brain (Grasso and Basil, 2009; Packard, 1972; Sasaki et al., 2010). The increase in computational power at this stage might have been selected to support arm coordination for locomotion and object manipulation (Godfrey-Smith, 2016; Packard, 1972), as well as navigation in the water column and basic learning processes (Grasso and Basil, 2009). Next, around 275

MYA the external shell was internalized (in the ancestors of cuttlefish and squid) or lost (in the ancestors of octopuses; Kröger et al., 2011; Tanner et al., 2017). It has been speculated that competition with marine vertebrates (Packard, 1972) was a driving factor that led to dramatic changes in the lifestyles of these animals (but see Aronson, 1991). First, the disappearance of the external shell allowed animals to occupy a wide array of ecological niches. Consequently, modern cephalopods are found in all marine habitats, from tropical to polar waters, and from benthic to pelagic niches (Jerep et al., 2014). Second, the loss of the protective shell likely increased predatory pressures drastically and consequently the rates of extrinsic mortality. These novel ecological conditions might not have only played a major role in the emergence of sophisticated biological adaptations (e.g. lens eye, chromatophores) but also in the co-evolution of cognitive sophistication and fast life history of cephalopods.

Which factors drove the evolution of intelligence in cephalopods?

The Ecological Intelligence Hypotheses (Chapter 1, for a recent review see Rosati, 2017) posits that intelligence evolves in response to challenging foraging niches. Cephalopods face ecological problems that seem comparable to those of apes and corvids. First, cephalopods exhibit a high level of diet generalism. For instance, South African common octopuses predate on more than 35 species, including crustaceans, gastropods, fishes, other cephalopods, and even conspecifics (Smith, 2003). Secondly, cephalopods prey on ephemeral resources that require substantial periods of exploration to be spotted and seized. In the wild, octopuses avoid visiting the same spots that were depleted on previous days (Forsythe and Hanlon, 1997; Mather, 1991b), suggesting that they might need to flexibly update their memory to optimize food-searching activities.

Finally, octopuses rely extensively on extractive foraging to feed on bivalves and extract prey from crevices. Extractive foraging is considered a key factor in the evolution of intelligence because these techniques i) are typically more costly than alternative foraging strategies (e.g. due to learning and higher predation risk associated with long-lasting procedures), ii) might require cognitive complexity (e.g. innovativeness) to be developed, and iii) allow individuals to cover the high energetic demands of large brains (Dunbar and Shultz, 2017; Rosati, 2017). Therefore, the ecological challenges faced by cephalopods indicate that the Ecological Intelligence Hypothesis can be an appropriate framework within which to study the evolution of intelligence in this group (Godfrey-Smith, 2013, 2016).

According to another influential view, the Social Intelligence Hypothesis, cognitive sophistication evolves as a tool to compete with, cooperate with, or learn from conspecifics (Chapter 1; for recent reviews see Byrne, 2018; Whiten, 2018; Whiten and van de Waal, 2017). Some cephalopod species live in simple social environments encompassing large but anonymous aggregations (e.g. squid), while others appear to experience only sporadic social interactions (e.g. octopuses; Boal, 1996; Schnell and Clayton, 2019). Thus, they do not engage in complex social bonds like those between mated partners in corvids (Emery et al., 2007) or group members in apes and cetaceans (Connor, 2007; Tomasello and Call, 1994). Building on this, one might conclude that cephalopods have not faced sufficiently challenging social problems to trigger the emergence of intelligence. However, our understanding of the social pressures experienced by different cephalopod species is still very sparse, and therefore a detailed evaluation of the Social Intelligence Hypotheses in this group might be premature.

Although octopuses are typically described as strictly solitary animals (Boal, 1996; Hanlon and Messenger, 2018), recent studies have reported long-term occupancy of clumped dens and frequent social interactions in some populations (Guerra et al., 2014; Scheel et al., 2016, 2017). Mated partners have been observed sharing dens and food in the 'Larger Striped Pacific Octopus' (Caldwell et al., 2015; Rodaniche, 1991), an elusive species that still needs to be assigned a scientific name. Furthermore, an important consideration here is that *differen*t kinds of social challenges might have participated in shaping cephalopod cognition. The mating system of these molluscs is characterized by high promiscuity (Franklin et al., 2012) and short reproductive periods (Anderson et al., 2002; Rocha et al., 2001). In addition, cannibalism is widespread among cephalopods (Ibáñez and Keyl, 2010). These animals have evolved several behavioural and morphological features (e.g. mating tactics, Marian et al., 2019; Sauer et al., 1992; mating position, Hanlon and Forsythe, 2008; Huffard and Godfrey-Smith, 2010; secondary sexual traits, Packard, 1961) to reduce the risk of cannibalism during mating. It is, therefore, possible that large brains supporting fast decision-making and flexible mating strategies (Brown et al., 2012; Huffard et al., 2010) might have emerged in cephalopods to navigate challenging reproductive environments, in which mating attempts can become fights for life.

A third hypothesis suggests that intelligence can emerge in response to the challenges exerted by predators (Chapter 1; Skelhorn and Rowe, 2016; van der Bijl et al., 2015; van der Bijl and Kolm, 2016; Zuberbühler and Byrne, 2006; Zuberbühler and

Jenny, 2002). Lacking a protective shell, cephalopods are highly vulnerable to a wide range of predators (e.g. cetaceans, seabirds, fishes, other cephalopods; Hanlon and Messenger, 2018; Sprogis et al., 2017) that differ substantially in their sensory ecology and hunting strategies (e.g. acoustically-, visually-, olfactory-guided). It is well accepted that cephalopod evolution has been influenced by high predation pressures exerted by marine vertebrates (Packard, 1972; Tanner et al., 2017). An iconic example of this is the sophisticated camouflaging behaviour of cephalopods, facilitating rapid and effective concealment from visual predators despite being colour blind (Chiao et al., 2011). Predator attacks can have dramatic fitness consequences and predator-prey interactions can be as cognitively challenging as intraspecific interactions (Byrne and Bates, 2007). Consequently, predation risk might have played a crucial role in the evolution of cephalopods' cognition.

Why did cephalopods not evolve slow life history?

Traditionally, the evolution of fast life histories in cephalopods has been discussed in terms of physiological constraints (e.g. inefficiency in fat storage metabolism, high energetic cost of jet swimming; O'Dor and Webber, 1986). Focussing on ultimate causes, there might be a complementary interpretation. Fast life histories and terminal reproduction are favoured in species with high extrinsic mortality because high investment in early reproduction is the safer strategy when chances of survival are low in adulthood (Crespi and Teo, 2002). By increasing the rates of unavoidable mortality due to predation, the loss of the protective shell might have favoured early senescence, thus preventing slow life history trajectories in cephalopods. The opposite trend might have characterized the evolution of large brained vertebrates. A few lines of evidence support this view.

First, cephalopod species experiencing reduced predation have unusually slow life histories. For instance, having retained the protective shell, nautiluses live up to 20 years and reproduce several times during their life (Wood and O'Dor, 2000). Furthermore, as highlighted by Godfrey-Smith (2016), the scarcity of predators in abyssal habitats (Seibel and Drazen, 2007) can explain why vampire squids have multiple reproductive cycles (Hoving et al., 2015) and why deep-sea octopuses have the longest egg-brooding period ever reported in the animal kingdom (>50 months, Robison et al., 2014). Second, a negative correlation between longevity and predatory pressure can also be seen in other groups, such as bivalves (Moss et al., 2016) and social insects (Keller and Genoud, 1997). Finally, in opisthobranch molluscs, several groups have lost their protective shell independently from cephalopods. These key events favoured the evolution of sophisticated defence strategies (e.g. crypsis, synthesis of toxic metabolites, storage of cnidocysts) and crucially, fast life histories in opisthobranchs (Wägele and Klussmann-Kolb, 2005). Interestingly, opisthobranchs did not evolve large brains and flexible behaviour. This difference between opisthobranchs and cephalopods might, in some cases, be explained by the increase in brain size and complexity that preceded the disappearance of the shell in the latter. Although some groups of opisthobranchs might have lost their shell after the development of alternative defence mechanisms, in other groups the disappearance of the shell might have pre-dated the emergence of alternative defence strategies (e.g. toxicity; Wägele and Klussmann-Kolb, 2005). Thus, lacking a sufficiently complex brain, opisthobranchs might have been constrained to evolve 'cognitively undemanding' adaptations to cope with novel ecological niches. In contrast, similar conditions might have favoured a further investment in brain growth in cephalopods. Consequently, the camouflage behaviours of cephalopods might require more enhanced cognitive complexity relative to the anti-predatory strategies in opisthobranchs.

In summary, the disappearance of the protective shell in the ancestors of cephalopods may have (i) produced a dramatic increase in unavoidable mortality thus selecting fast life histories and (ii) in parallel facilitated widespread colonization of complex niches, thus driving cephalopods to cope with novel challenging problems. Cephalopod flexible behaviour and large brains might have emerged primarily in response to predation and complex feeding contexts. However, social challenges, particularly during mating, may have acted as additional selective pressures in their cognitive evolution. Thus, indicators of intelligence may have evolved in cephalopods and large-brained vertebrates through alternative routes, in response to partially different pressures and in association with opposite life histories.

6.4: BEHAVIOURAL PARADIGMS TO TEST COMPLEX COGNITION IN THE OCTOPUS

As pointed out earlier, the only way to test whether convergent evolution between cephalopods and large-brained vertebrates extends beyond behavioural similarities is to conduct a systematic investigation of the cognitive mechanisms underpinning cephalopods' behaviour. To this end, it is crucial to select promising model species among cephalopods and devise appropriate paradigms that will allow researchers to measure these animals' cognitive complexity in different domains. An intriguing candidate for this line of research is the common octopus. This octopus is an established model species for the study of learning and problem solving in cephalopods (Boycott, 1954; Fiorito et al., 1990; Fiorito and Chichery, 1995; Mackintosh and Mackintosh, 1963; Richter et al., 2016; Wells, 1959) due to its remarkable manipulative inclination and neophilia (e.g. Kuba et al. 2003, 2006). In what follows, I describe novel behavioural paradigms that can be used to investigate physical, future planning and social cognition in the octopus. Importantly, the proposed experiments represent a tool to collect baseline data. As discussed in Chapters 3, 4, and 5 (see also Chapter 7), it is problematic to draw solid conclusions on the cognitive abilities of a species based on a single study. Thus, in case the paradigms presented here will prove to be effective to test for instance, social cognition in common octopuses, then results should be considered as indicative rather than as final. To corroborate the findings, it will be crucial to conduct further research in the octopus, and especially to test the robustness of the results through replication studies and to employ a range of different tasks to investigate the same cognitive capacity in this species.

6.4.1: TOOL USE

Octopuses use a variety of tools for different purposes, including stones to block the entrance of their dens, coconut shells to assemble movable dens and water jets to distance scavenger fish (Finn et al., 2009; Mann and Patterson, 2013; Mather, 2016). According to anecdotal observations octopuses also engage in tool-mediated foraging: common octopuses have been observed to insert a pebble in between the two shells of large bivalves (*Pinna nobilis*), thus preventing the mussel to seal up the shells, and consequently to prey the mussel by pulling open the shells (Pliny the Elder, 1983; Power, 1857). To date, octopuses' ability to use tools has never been tested in the laboratory, thereby it is not clear how flexible the cognitive underpinnings of these behaviours are. Here I propose two experimental paradigms to investigate whether octopuses can i) learn a novel tool use behaviour to solve an artificial task, and ii) flexibly achieve the same goal through different strategies, namely by employing perceptually different – but functionally equivalent – objects as tools, or by using both solid objects and water as tools. Both paradigms require octopuses to acquire an out-of-reach reward by using a tool.

EXPERIMENT 6.1

Experimental Questions

i) Can octopuses learn a novel tool use behaviour to solve an artificial task?
ii) Can octopuses employ different tool use strategies to solve the same task?

Set-up

The apparatus consists of a small plastic platform suspended above the octopus' tank through a fishing line (Fig. 6.2). A baited container (i.e. a two-parts hollow ball) is placed on the apparatus. To solve the task, the octopus has to use a tool to knock down the container.

Protocol and Predictions

Familiarization: The aim of the Familiarization is to give the octopus the opportunity learn that the food container is baited and detachable from the platform. Thus, the platform is suspended a few centimetres below the water surface so that the octopus can directly grab the food container by extending one of its arms (Fig. 6.2a). After having acquired the container and fed on the bait during five consecutive trials, the octopus proceeds to the next stage.

Training: The Training consists of two stages. The aim of Stage 1 is to foster an association between the tool and the reward, i.e. the octopus should learn that the out-of-reach food container can be acquired by using an object as a tool. The aim of Stage 2 is to allow the octopus to learn the specific sequence of actions required to knock down the food container through an object. In both training stages, the apparatus is suspended above the water surface such that the food container cannot be reached without a tool. A plastic rod with both ends sealed is provided as a tool. To ensure the vertical buoyancy of the rod, a weight is fixed inside it close to one end. In Stage 1, the rod is connected to the platform through a plastic linker (Fig. 6.2b). This set-up facilitates the successful solving of the task because any manipulation of the tool by the octopuses (e.g. pulling downward or pushing upward) causes the container to fall from the platform. In Stage 2, the rod is loose (Fig. 6.2c) such that the octopus must knock the container by pushing the rod upward. After five consecutive successful trials in each training stage, the octopus proceeds to the test.

If the octopus can pass the Training, then results would demonstrate that the octopus is capable of acquiring a novel tool use behaviour.

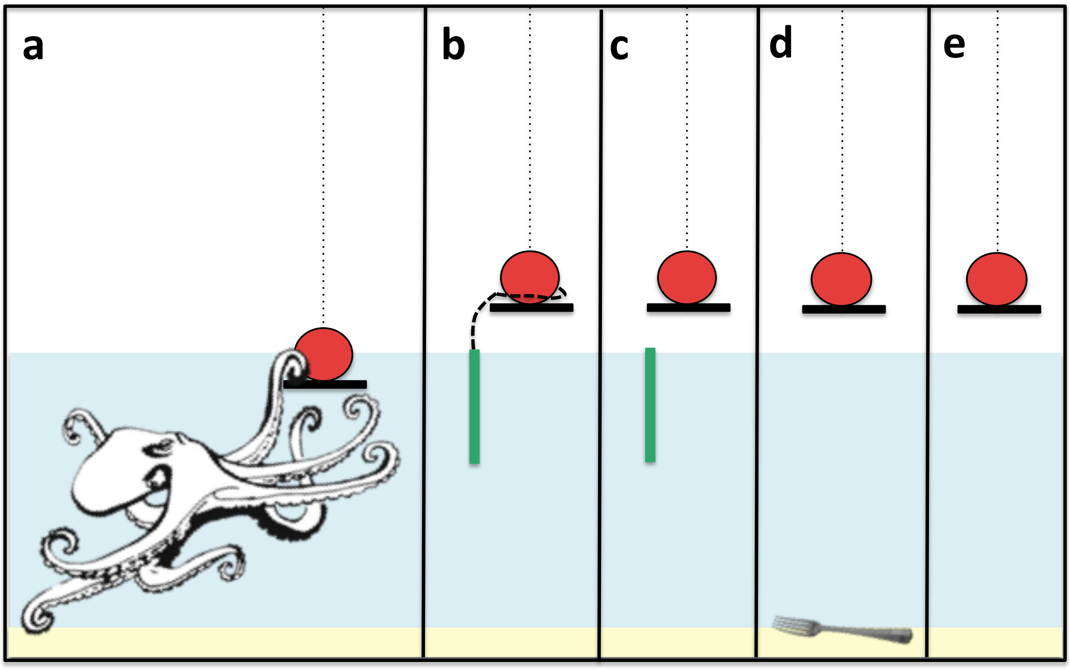

Figure 6.2: Schematic representation of Experiment 6.1. In the Familiarization (a), the baited container is in-reach. In the Training (b, c), a plastic rod (green line) is provided as tool. The rod is connected to the container in Stage 1 (b), but it is loose in Stage 2 (c). In Test 1 (d), a perceptually different object is provided as tool. In Test 2 (e) no to is provided: the octopus can only knock down the baited container through water squirts (water as tool).

Test: The tests aim at investigating the cognitive flexibility of tool use behaviour in the octopus. Specifically, Test 1 investigates whether octopuses can acquire the reward from the same apparatus by using a novel and perceptually different object as tool. Test 2 aims at testing whether octopuses can solve the task through an alternative strategy, namely by using water as tool.

In Test 1, the octopus is provided with a novel tool, namely a loose object that differs from the tool used in the Training in colour, shape and material. Thus, test 1 is a transfer task for the behaviour acquired during training. Positive performance in Test 1 would show that the octopus can solve a familiar task through a novel object, thus indicating some level of cognitive flexibility and capability to generalize to use perceptually different – yet functionally equivalent – tools.

In Test 2, no tool is provided such that the octopus can knock down the baited container only by aiming water squirts (water as tool) at the container. If the octopus is not capable of spontaneously devising this alternative strategy over 10 trails, i.e. if no attempt to solve the task by using water is observed, demonstrative trials are conducted to facilitate the emergence of the behaviour. This is because the demonstrative trials provide the opportunity for the octopus to see that the food reward can be knocked down by using water. Here, the experimenter introduces one hand in the tank holding a squeezable plastic receptacle out of the view of the octopus. By compressing the object, the experimenter directs water jets toward the apparatus thus causing the food container to fall in the water. Subsequently the octopus is allowed to recover the container and to feed on the bait. Following five demonstrative trials, octopuses are tested again.

If the octopus can pass Test 2, then results would support remarkable cognitive flexibility because i) the sequence of actions required to knock down the baited with water jets differ substantially from that required to solve the task through a solid object; ii) the octopus was not previously trained to solve the task by using water as a tool, and iii) octopuses are not known for squirting water jets to acquire food.

Pilot

To evaluate whether the paradigm of Experiment 1 is appropriate for investigating tool use in the octopus, I have conducted a pilot study involving the Familiarization and Training (Stage 1). Given the exploratory aim of the pilot, and because of time constraints, I did not employ a standardized protocol but rather presented individual octopuses with the set-up and observed the behavioural responses of the animals. I tested two common octopuses (approximately 300 g). The study was carried out in July 2017 at the Stazione Zoologica Anton Dohrn, Napoli, Italy, in collaboration with Dr. Graziano Fiorito. Preliminary results were promising: both octopuses i) consistently grabbed the baited container when it was in reach (Familiarization), and ii) were capable of solving Stage 1 training trials: they could acquire the out-of-reach container by pulling a tool that was connected to the container (Fig. 6.3). Therefore, the paradigm appears to be appropriate to investigate tool use behaviour in octopus.

Figure 6.3: A common octopus (*Octopus vulgaris*) solving a training trial (Stage 1). The animal is pulling a tool (green upholstered metal wire) that is attached to the apparatus to acquire the baited container.

EXPERIMENT 6.2

Experimental Questions

i) Can octopuses learn a novel tool use behaviour to solve an artificial task?

ii) Can octopuses employ different tool use strategies to solve the same task?

Set-up

The apparatus consists of a clear plastic pipe with one sealed end and one baited lateral chamber (Fig. 6.4). The apparatus is fixed on a heavy platform. An obstacle – either a stone or a stinging anemone attached on the base – is positioned in front of the non-sealed opening of the pipe. To solve the task, the octopus has to displace the obstacle and grab the food reward by inserting one arm inside the apparatus.

Protocol and Predictions

Familiarization: The aim of the Familiarization is to give the octopus the opportunity to learn the basic requirement of the task, i.e. to remove the obstacle to gain access to the reward. Here, a stone is used as the obstacle. The octopus can easily displace the obstacle by grabbing it with the arms and moving it away. After five consecutive successful trials, the octopus proceeds to the Training.

Training: The Training encompasses two stages and involves a stinging anemone as the obstacle. In Stage 1, the octopus should learn that the obstacle can be displaced only by using an object as a tool because a direct physical contact with the obstacle would result in a painful experience. In Stage 2, the octopus should learn the specific sequence of actions required to remove the obstacle: it should hold the object and push it against the obstacle to displace it. Following the basic design of Experiment 6.1, the two stages of the Training differ in whether or not the object provided as a tool is loose. In Stage 1, the tool (e.g. a plastic stick) is attached to the obstacle through a fishing line such that any displacement of the tool would also cause the displacement of anemone. In Stage 2, the tool is loose; the octopus has to hold the tool and push it against the anemone to remove the obstacle. After five consecutive successful trials in each training stage, the octopus proceeds to the test.

If the octopus can pass the Training, then results would demonstrate that the octopus is capable of acquiring a novel tool use behaviour.

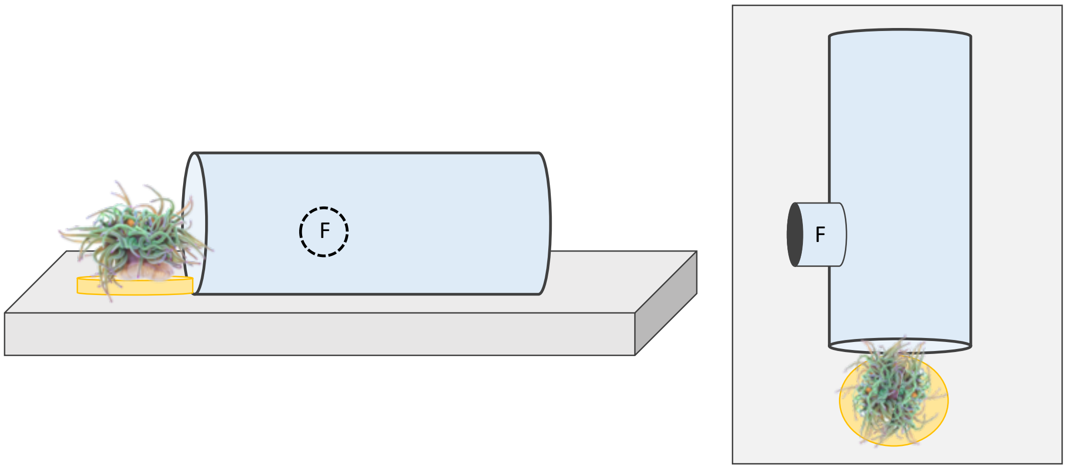

Figure 6.4: Schematic representation of the apparatus used in Experiment 6.2. The apparatus is visible from a lateral view (left) and top view (right). The apparatus consists of clear Perspex pipe with one sealed end, and a baited lateral chamber (F). An obstacle (e.g. a stinging anemone attached on a plastic disc) is placed in front of the opening of the pipe, thereby blocking the access to the bait.

Test: The aim of the Test is to investigate the cognitive flexibility of tool use behaviour in the octopus. In particular, the Test investigates whether octopuses can solve a familiar task by using a novel and perceptually different object as a tool or through an alternative strategy, namely by using water as a tool.

In the Test, no tool is provided. The octopus can solve the task through two alternative strategies. First, the octopus can displace the obstacle by using a perceptually different tool, namely a pebble that together with sand from the substrate of the octopus' tank. Second, the octopus can displace the obstacle by aiming water squirts at the anemone. If the octopus is not capable of spontaneously performing this alternative strategy (nor to use a pebble as a tool), demonstrative trials (as described in Experiment 6.1) are conducted to facilitate the use of water as a tool.

Successful performance in the Test, through either strategy, would support remarkable cognitive flexibility. In contrast to Experiment 6.1, here the tool that can be used in the Test (i.e. the pebble) is not presented together with the apparatus in the trials. This procedure requires higher cognitive flexibility than that of the transfer task (Test 1) in Experiment 6.1. The octopus cannot solve the task by following a simple rule – 'any novel object provided can be used to acquire the reward' – instead the octopus must spontaneously consider that a familiar object that is always available (i.e. the pebble) is functionally equivalent to the training tool, and therefore can be used to solve the task.

As in Experiment 6.1, solving the task by using water as tool requires cognitive flexibility because: i) the sequence of actions required to displace the obstacle through water jets differ substantially from that required to solve the task through a solid object; ii) the octopus was not previously trained to solve the task by using water as a tool, and iii) octopuses are not known for squirting water jets to acquire food.

6.4.2: FUTURE PLANNING

Jozet-Alves et al. (2013) reported that cuttlefish can remember the what, where and when features of past events (episodic-like memory). Given that episodic memory and future planning are thought to be based on the same cognitive machinery (Clayton et al., 2003; Suddendorf and Corballis, 2007), this evidence raises the possibility that cephalopods are capable of prospection cognition (see also Billard et al., 2020). The carrying of coconut shells by veined octopus (Finn et al., 2009) is in line with this hypothesis because the transport of tools has a cost (e.g. increased risk of being spotted by a predator due to the conspicuous locomotion) and it does not provide benefits when the behaviour is performed but only in the future, i.e. the tools do not protect the octopus while being carried but they can be assembled into a safe shelter after a new location is reached. Building of Finn et al. (2009)'s observations, here I propose a paradigm that investigates whether octopuses choose to carry a movable den to a new location only when this behaviour results in a future benefit. To this end, octopuses are exposed to two locations: one *Safe* location where a shelter is available and no predator is visible, and one *Dangerous* location where no den is available and predators can be seen. As a result of these manipulations, the movable den is beneficial to the octopus only if it is carried into the *Dangerous* location.

EXPERIMENT 6.3

Experimental Question

i) Do octopuses carry a movable den only when it provides benefits in the future?

Set-up

The octopus' tank is divided in three compartments through opaque PVC walls: a Resting compartment where the octopus is housed and two smaller Testing compartments that can be accessible during the experiment (Fig. 6.5). A den that can be carried around (e.g. a plastic pipe, two coconut shells) is positioned in the Resting compartment, whereas an unmovable den (e.g. two heavy bricks arranged to form a cavity) is placed in one Testing compartment (*Safe* compartment) and no den is placed in the other (*Dangerous* compartment). The octopus can move from the Resting compartment to each of the two Testing compartment through two holes in PVC wall. The holes are adjustable, i.e. they can be opened at different sizes or completely closed. A video screen is positioned outside the octopus' tank, allowing the animal to watch videos when it is housed in the Testing compartments. Videos are used to manipulate the perceived predatory risk associated in each Testing compartment: a natural predator (e.g. a grouper, moray eel) is showed in trials in which the octopus is confined in the *Dangerous* compartment, while a non-threatening species (e.g. dreamfish) is used in trials in which the octopus is confined in the *Safe* compartment.

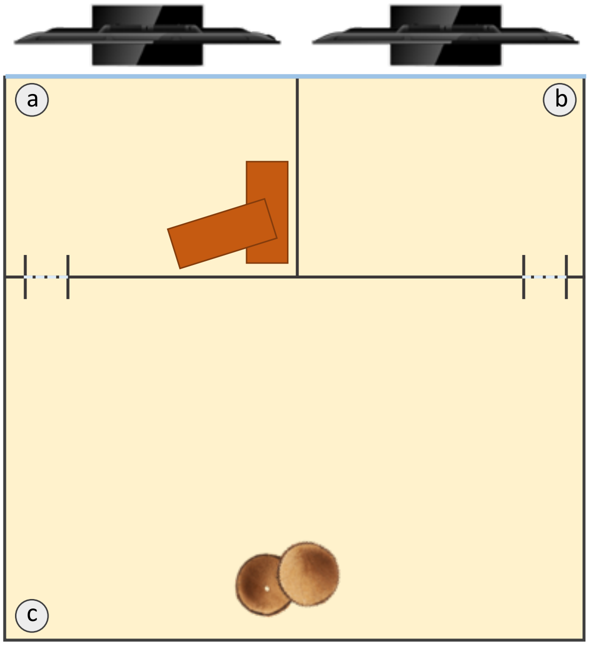

Figure 6.5: Top view schematic representation of the set up used in Experiment 6.3. The experimental tank is divided in two Testing compartments (a, b) and one Resting compartment (c). An unmovable den (e.g. two bricks arranged to form a cavity) is available in the *Safe* compartment (a). No shelter is available in the *Dangerous* compartment (b). A movable den (e.g. two coconut shells) is available in the Resting compartment. Videos are presented to the octopus when it is housed in Testing compartments, through video screens positioned outside the tank.

Protocol and Predictions

The experiment encompasses an Experience phase (three consecutive days) followed by a Test phase (one day).

Experience phase: The aim of the Experience phase is to give the octopus the opportunity to learn that i) a shelter is available in the *Safe* compartment but not in the *Dangerous* compartment, and ii) predators can be found only in the *Dangerous* compartment.

In the Experience phase, the octopus receives two trials per day, one in the morning and one in the afternoon. On each trial, the octopus is allowed to enter either the *Safe* or the *Dangerous* compartment through one hole in the wall. The octopus cannot carry the movable den from the Resting compartment because the object cannot fit through the hole. Once locked inside the Testing compartment, the octopus is given a live crab and allowed to eat the prey during two hours[12]. Crucially, only in the *Safe* compartment does the octopus have a safe shelter to consume the prey. During this time, short videos are presented (e.g. a 5 minutes video is played 3 times/hour) through the video screen. A natural predator (*Dangerous* compartment) or a non-threatening species (*Safe* compartment) is showed in trials in which the octopus is confined in the

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[12] Octopuses require substantial time to feed on crustaceans and bivalves. Two hours is an appropriate time frame for an octopus to consume a crab.

compartment. At the end of each trial, the experimenter re-opens the hole in the wall and induces the octopus to return to the Resting compartment through gentle movements of one hand. The octopus experiences both Testing compartments on each Experience day in a randomized order. For instance, on day 1, the octopus may be confined in the *Safe* compartment in the morning and in *Dangerous* compartment in the afternoon, whereas, the animal may experience the alternative order on day 2. At the end of the Experience phase, the octopus has experienced each Testing compartment three times.

Test: The Test aims at investigating whether the octopus chooses to transport the movable den only when the den provides a future benefit, i.e. a safe shelter to consume a prey in a location where no den is available but predators can be spotted. On day 4 of the experiment, the octopus receives two test trials: one trial in the *Safe* compartment (e.g. in the morning) and one trial in the *Dangerous* compartment (e.g. in the afternoon). The same procedure used in Experience trails is also employed in Test trials except that: i) video stimuli are not presented, and crucially ii) the holes in the wall are opened more widely such that the movable den can fit through it. Therefore, in contrast to the Experience phase, here the octopus has the opportunity to carry the movable den into each Testing compartment and use it as a shelter during the trial.

If the octopus can remember that in the *Dangerous* compartment no shelter is available and predators can be found, it is expected to carry the movable den from the Resting compartment only in the Test trial in the *Dangerous* compartment. In contrast, the octopus should not transport the den into the *Safe* compartment because in this location an unmovable shelter is available and predators were never encountered. The expected performance would be consistent with the hypothesis that octopus can plan for the future and demonstrate that the carrying of dens is a behaviour that can be flexibly adjusted according to future needs. Importantly, the transport of the movable dens into the *Dangerous* compartment may represent the expression of prospection because i) the behaviour provides no benefit while it is performed, but only after it has been completed, ii) octopuses were not trained to exhibit the behaviour prior to the test. However, if octopuses will be capable to solve the task, follow-up studies should be conducted to exclude the possibility that throughout the Experience phase the octopus could have developed a negative association with the *Dangerous* compartment (e.g. stress caused by lack of shelter), and consequently it may have carried the movable dens in this compartment only because the object has a positive value, without the need for any prospective ability.

6.4.3: SOCIAL COGNITION

Octopuses are most often described as solitary animals exhibiting weak social tolerance and cannibalistic attitudes (Hanlon and Messenger, 2018; Ibáñez and Keyl, 2010; Schnell and Clayton, 2019), thereby one may not expect them to have evolved complex and flexible social cognition. However, a number of studies have reported populations living in high densities in the wild (Guerra et al., 2014; Hanlon and Messenger, 2018; Scheel et al., 2016, 2017), thus challenging the idea that octopus may rarely encounter conspecifics and face social problems (e.g. competition over shelters). Experimental evidence also suggest that octopus may learn vicariously (Fiorito and Scotto, 1992), individually recognize conspecifics (Tricarico et al., 2011), and maintain social hierarchies in artificial settings (Cigliano, 1993). Further, the apparent cooperative hunting with fish (Unsworth and Cullen-Unsworth, 2012; Vail et al., 2013) may represent an additional scenario in which flexible cognition is required to interact with another individual, namely a heterospecific. Here I present two novel protocols to explore octopuses' social cognition in a competitive (Experiment 6.4) and a cooperative context (Experiment 6.5). Building on Hare et al. (2000)'s study in chimpanzees, Experiment 6.4 investigates whether octopuses can maximize individual benefit by responding to the visual perspective of a competitor. Experiment 6.5 relies on a novel paradigm in which two octopuses are presented with hidden rewards that can only be acquired through the synchronized actions of the two individuals.

EXPERIMENT 6.4

Experimental Question

i) Can octopuses adjust their behaviour according to the visual perspective of a conspecific?

Set-up

The testing tank is divided into three areas: a narrow central area delimited by two clear Perspex walls, and two large adjacent compartments, in which two octopuses are individually housed (Fig. 6.6). A den is available in each compartment. Food rewards (e.g. pieces of anchovy) are presented in the central area. The bait is attached to a plastic ball which is fixed to one end of a rod (Fiorito and Scotto, 1992), therefore being easily manoeuvrable. Octopuses can reach the food rewards through holes (spaced 20 cm) in the Perspex walls. Importantly, the experimenter can manipulate whether the bait is visible or not visible to the octopuses by adjusting the orientation of the ball. Specifically, the ball can be oriented such that the bait faces one octopus, thus being not visible to the other octopus; alternatively the rod can be spun 90°, thus resulting in the bait being visible to both octopuses (Fig. 6.6).

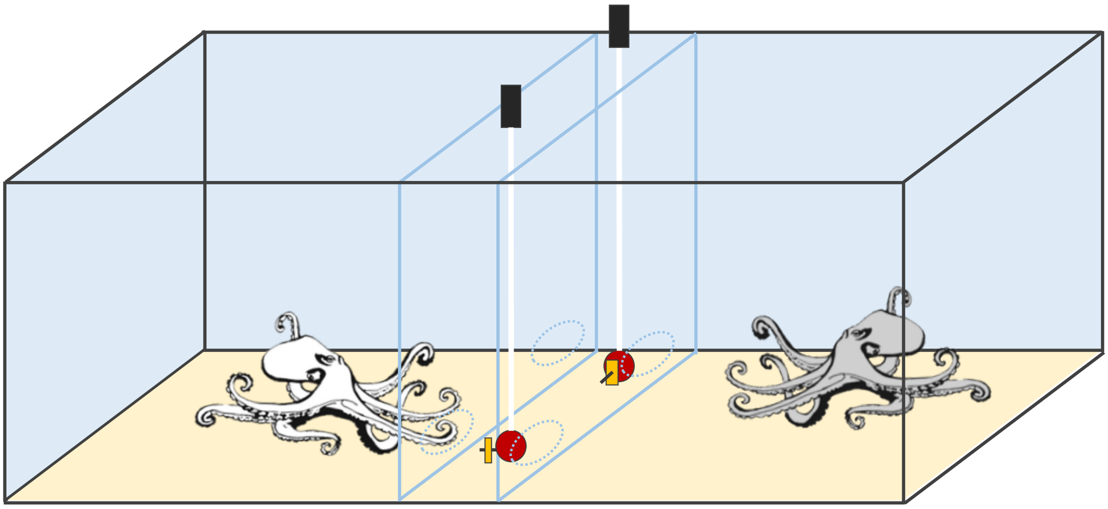

Figure 6.6: Schematic representation of the set-up of Experiment 6.4. Two clear Perspex panels divide the experimental tank in two compartments where octopuses are housed individually and one central area where baits (yellow square) are presented. The bait is attached to a plastic ball (red circles) at the end of a rod (white line). The rod has a handle (black square). The ball can be oriented so that the bait is visible to both octopuses, i.e. the bait faces the other ball (upper bait). Alternatively (lower bait), the ball can be oriented so that the bait faces the subordinate octopus (white) and therefore it is only visible to the subordinate but not to the dominant octopus (grey). Octopuses can acquire the baits through the holes in the Perspex panels.

Protocol and Predictions

Familiarization: This phase is conducted to allow the octopus to gain familiarity with the set-up and learn that it can acquire food rewards attached to the plastic balls. One octopus is moved into the experimental tank and given 15 minutes to acclimatize before the start of the testing. In each trial, two balls are presented in the central area. The balls are oriented so that the baits are visible to the octopus. After the animal has reached the baits through the holes in the Perspex wall, the balls are removed. Sessions of ten trials are conducted. The octopus proceeds to the next stage after successfully getting the bait in five consecutive trials.

Test: The Test aims at investigating whether, when presented with two identical food rewards, subordinate octopuses take into account the visual perspective of a dominant conspecific, thereby choosing preferentially the reward that cannot be seen by the competitor. Trials involve an Acclimatization phase followed by a Testing phase. At the start of the Acclimatization, two octopuses are moved into the experimental tank and individually housed in the two compartments. At this stage, an opaque Perspex panel is positioned into the central area to temporarily prevent visual interaction between the two octopuses. Octopuses can acclimatize to the new tank for 15 minutes. Next, the opaque panel is removed. For 15 minutes, social interactions (e.g. agonistic/avoidance behaviours) are observed to establish the dominance relationship between the individuals. In case of limited or no interactions (e.g. if octopuses remain in their dens), a live crab may be presented in the central area to induce the octopuses to move close to the central area. Octopuses cannot seize the prey: the crab (attached to a cotton line) is promptly removed from the tank before an octopus can grab it. Next, the Testing phase starts. An additional clear Perspex wall is introduced in the compartment housing the dominant octopus to temporarily prevent it from reaching into the central area. When both octopuses are in a standardized position (i.e. at their dens), two baited balls are presented simultaneously inside the central area, in correspondence of the holes in the Perspex walls. Octopuses have to choose which bait to grab because the baits are spaced too far apart to be grabbed together at the same time. The subordinate octopus is given a head start: after it has left the den and is in proximity (e.g. 10 cm) of the central area, the additional wall is removed so that the dominant octopus can also reach the baits. The trial ends when both baits are taken by the octopuses and the two balls are subsequently removed from the tank. Pairs of octopuses receive sessions of ten trials, with an inter-trial-interval of 2 minutes.

Octopuses are tested in two conditions. In the *Visible-Visible* condition, the balls are oriented so that the two baits are visible to both octopuses. In the *Visible-Non visible* condition, the balls are oriented so that one bait is visible to both octopuses but the other bait is visible only to the subordinate (Fig. 6.6). Within each session, octopuses receive five trials of each condition in a pseudorandomized order, i.e. the same condition is not performed for more than two consecutive trials. In *Visible-Non visible* trials the relative position of the two balls (i.e. left/right) is randomized. The bait selected by the subordinate octopus is scored in each trial.

If octopuses can respond to the visual perspective of conspecifics, subordinate octopuses should prefer the bait that cannot be seen by the dominant in the *Visible-Non visible* condition more often than in the *Visible-Visible* condition.

EXPERIMENT 6.5

Experimental Question

i) Can octopuses solve a problem solving task cooperatively?

Set-up

The experimental tank comprises two individual compartments divided by a clear Perspex wall (Fig. 6.7). The wall allows the housing of the apparatus in between the two compartments. The apparatus consists of a rectangular flat box made of clear Perspex. The box has two crevices in the ceiling, at the opposite sides of the box. One live crab is hidden in each of the crevices. A weight (e.g. a brick) is placed on the top of the apparatus to cover the opening of the crevices. To gain access to the crab, the octopus must displace the weight and insert the arms inside the crevice. The weight can be displaced in different directions: the octopus can drag the weight sideways, push it back (i.e. toward the adjacent compartment) or pull it toward itself.

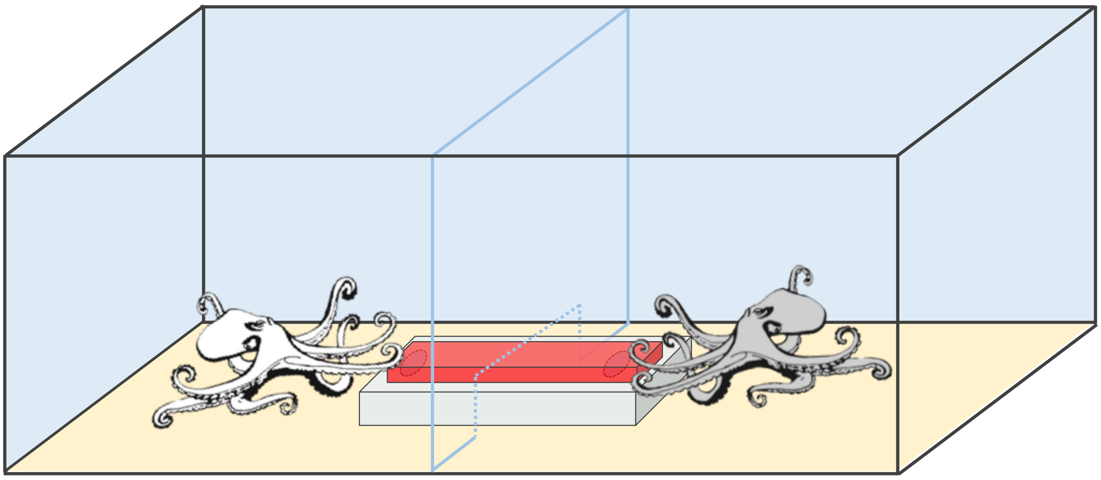

Figure 6.7: Schematic representation of the set-up of Experiment 6.5. A clear Perspex wall divides the experimental tank in two individual compartments. The apparatus consists of a flat clear box (grey parallelepiped) with two baited cavities (circles) covered by a weight (red parallelepiped).

Protocol and Predictions

Familiarization: A Familiarization is conducted to allow the octopus to learn the basic requirement of the task, i.e. to displace the weight to gain access to the prey. In this phase, octopuses are tested individually in the experimental tank. After 15 minutes of acclimatization, the octopus is presented with the apparatus. Only one crevice is baited. The weight is light enough to be removed by a single octopus. The octopus proceeds to the test after five consecutive successful trials.

Test: The Test aims at investigating whether octopus can solve a foraging task cooperatively. In the test, two octopuses are individually housed in the two compartments. The animals are allowed to acclimatize to the experimental tank and the sight of the conspecific for 15 minutes. Octopuses cannot interact physically because an additional clear wall (with no space for housing the apparatus) is positioned in between the two compartments. Next, this additional wall is removed and the apparatus is presented. Both crevices are baited, i.e. each octopus has the opportunity to gain access to one crab. The weight covering the crevices is as heavy as is required for two octopuses to displace it together. To solve the task, octopuses have to synchronize their actions, either through the same strategy (e.g. sliding the brick toward left) or complementary strategies (i.e. one octopus pulls and the other pushes the weight simultaneously). Each pair of octopuses receives a single trial per day. If two octopuses cannot solve the task in five consecutive trials, the individuals are assigned to a different pair. Positive results in the Test would show that, despite being solitary creatures, octopuses can attend to a conspecific when this leads to a positive outcome.

6.5: CONLCUSIONS

In this Chapter I focused on the second objective of my thesis, namely the attempt to lay theoretical and methodological groundwork for the study of convergence cognitive evolution between cephalopods and large-brained vertebrates, such as the corvids I focussed on in Chapters 2 to 5. Following a review of the most striking evidence of behavioural complexity in cephalopods, I proposed that current evidence may be sufficient to hypothesize a first-level convergence (i.e. behavioural convergence) among these groups. Subsequently, I discussed cephalopods' cognitive evolution in relation to the main hypotheses for the evolution of intelligence in vertebrates and suggested that ecological factors (i.e. predatory and foraging pressures) may have played a key role in the emergence of cognitive sophistication together with fast life history. Finally, I presented a number of novel paradigms that can be used in the future to investigate cognitive complexity in the octopus, and thus to explore whether cephalopods' convergence with vertebrates may extend to a deeper level of analysis.

In the final Chapter of this thesis, I discuss the implication of my empirical findings in the Eurasian jays and theoretical considerations regarding cephalopods. I conclude by evaluating future steps in the study of convergent cognitive evolution in corvids and cephalopods.

Chapter 7:
General Discussion

The general aim of this thesis was to gain further insights into the process of convergent cognitive evolution: the independent emergence of comparable cognitive sophistication in distantly related lineages. To this end, I decided to focus on corvids and cephalopods, two lineages that evolved complex and flexible behavioural repertoires despite the fact that their evolutionary histories and brain structures differ dramatically from those of the most established model group for the study of intelligence, namely primates (Emery and Clayton, 2004; Mather and Dickel, 2017; Schnell and Clayton, 2019; Seed et al., 2009a). As discussed in Chapter 1, the study of cognitive convergence is a challenging task because i) cognition can only be measured through proxies, ii) intelligence (or complex cognition) is not clearly defined, and iii) the principle of convergence is elusive: a trait exhibited in different groups can be said to be convergent or divergent depending on the level at which the trait is analysed. In this thesis I have adopted Seed (2007)'s hierarchical framework to investigate cognitive convergence. According to the author, at the first and more superficial level, convergence (i.e. behavioural convergence) can be hypothesized if two lineages exhibit behaviours that seem comparable complex and flexible. At the second level of analysis, cognitive convergence between two groups can be invoked when their behavioural flexibility is not underpinned by hardwired predispositions or simple learning processes. Finally, at the third and deeper level, cognitive convergence occurs when similar cognitive mechanisms underlie behavioural flexibility in distantly related groups.

In the introduction of this thesis (Chapter 1) I have considered at which level of Seed (2007)'s framework the currently available evidence supports a case of convergent cognitive evolution between corvids and apes, as well as between cephalopods and large-brained vertebrates. With regard to the former case, I argued that current evidence is consistent with a second-level convergence, yet not sufficient to support a third-level convergence. In particular, I contended that the currently available evidence limits the proper evaluation of Emery and Clayton (2004)'s proposition, namely that corvids may share with apes a flexible and domain-general cognitive tool kit. This is because, in contrast to apes, evidence of cognitive sophistication *within the same species* of corvids is limited. Consequently, it is not possible to distinguish whether the cognitive complexity reported at the level of the corvid family results from complementary cognitive specializations in different species/subgroups or from a domain general cognitive tool-kit shared by individual species of the corvid family as hypothesized by Emery and Clayton (2004; cf. Seed 2007). With regard to the latter case, I highlighted that a proper assessment of cognitive convergence between cephalopods and large-brained vertebrates is currently problematic because cephalopods' cognitive sophistication is still largely untested, and the process (e.g. evolutionary pressures) selecting for large brain and flexible behaviour in cephalopods has been largely overlooked. Building on these considerations, the present thesis was guided by two objectives. The first objective was to take one step further in understanding how deep the cognitive convergence between corvids and apes may be. The second objective was to investigate the potentials of cephalopods as a novel model group for the study of convergent cognitive evolution.

In what follows, I will summarize the outcomes of each chapter and discuss the implications of my findings, relating back to the two objectives of my thesis. Finally, I will provide inputs for future research. Following the general structure of the thesis, I will first discuss the research on corvids and then that on cephalopods.

7.1: CORVIDS

7.1.1: SUMMARY OF RESULTS

To address my first objective, in Chapters 2 to 5 I investigated three cornerstones of cognitive sophistication – physical problem solving, future planning and social cognition – in the Eurasian jay (Tab. 7.1), in an attempt to investigate whether the hypothesis that corvids are endowed with a flexible and domain general cognitive tool-kit (Emery and Clayton, 2004) is supported in this species.

In **Chapter 2**, I focused on tool use behaviour, perhaps the most iconic expression of physical problem solving. Building on previous research on rooks (Bird and Emery, 2009), I employed two object-dropping tasks – requiring the bird to insert a tool (e.g. stone) into a vertical tube to acquire a reward – to test whether these jays can select functional tools according to two physical properties, namely size (Experiment 2.1) and shape (Experiment 2.2). Additionally, I conducted a third experiment

(Experiment 2.3) aimed at exploring jays' capability of using novel tools (sticks) to solve a task involving a familiar apparatus. Consistently across the two selectivity tests, I found that jays could not spontaneously adjust their selection according to the functionality of the tools. In Experiment 2.1, jays initially preferred large stones as tools, regardless of whether these objects could fit or could not fit into the apparatus. However, jays progressively developed a preference for the small tool, which was functional in all trials, thus supporting a previous finding that these corvids can *learn* to choose functional tools on the basis of density (Cheke et al., 2011). In Experiment 2.2, jays exhibited a preference for long stones (over round stones) but tended to achieve the correct manipulation only when required, i.e. they oriented vertically the long stone when this was necessary for the tool to fit into the apparatus. Most often however, the correct orientation of the long stone was achieved after a few unsuccessful attempts of insertion, so that it is likely that this performance may have resulted from trial-and-error, in the lack of a full understanding of the objects' properties and functionality. In Experiment 2.3, jays were able to use sticks and adopt a novel technique on the same object-dropping apparatus, thus providing the first evidence that Eurasian jays can use sticks as tools. Taken together, the results of these experiments may suggest that Eurasian jays are endowed with limited tool selectivity abilities but that they can nonetheless use different kinds of tools to achieve the same goal, thus indicating some degree of cognitive flexibility.

Table 7.1: Contribution of the present thesis to the state of art of Eurasian jays' cognitive complexity in physical problem solving, future planning and social cognition. The 'Reliability' column outlines whether a given effect was corroborated by subsequent studies (✓), is supported by a single study (no sign), or was not supported by subsequent studies (✗).

Domain	Reported Effects	Reliability	References
Physical Problem Solving	Learn to use tools (object dropping tasks) through training	✓	Cheke et al. 2011; Miller et al. 2016; Chapter 2
	Learn to select functional tool based on density		Cheke et al. 2011
	Learn to select functional tool based on size and shape		Chapter 2
	Solve a familiar task through novel tools (sticks) and alterntive strategies		Chapter 2
Future Planning	Distribute caches to maximize future benefit, in line with planning abilities	✗	Checke and Clayton 2012, but see Chapter 3
	No evidence that Ej' future-oriented caching is underpinned by either predisposition or prospection abilities		Chapter 3
Social Cognition	Protect caches by responding to the visual perspective of a conspecific	✗	Legg and Clayton 2014; but see Chapter 4 and 5
	Protect caches by responding to the acoustic perspective of a conspecific		Shaw and Clayton 2013
	Protect caches by responding to the current desire of a conspecific	✗	Ostojic et al. 2017; but see Chapters 4, 5, Crosby 2019
	Adjust food sharing by responding to the current desire of the pair mate	✓	Ostojic et al. 2013, 2014, 2016
	No evidence that Ej can integrate cues about others' desires and perspectives to protect their caches		Chapter 4

In **Chapter 3,** I turned my attention to a second cornerstone of cognitive sophistication, namely future planning abilities. Previous research indicated that jays adapt their caching behaviour according to future needs. Specifically: i) de Kort et al. (2007) showed that California scrub-jays can learn where not to cache when they are provided with one tray in which caches are always pilfered and another tray in which caches are always returned; ii) Raby et al. (2007) found that scrub-jays tend to cache more in locations where food will be absent on the next morning or preferentially cache a specific type of food (relatively to another type of food) in a location where that food will not be available on the next morning; iii) Correia et al. (2007) and Cheke and Clayton (2012) reported that scrub-jays and Eurasian jays select what food to cache according to their motivational state at the time of recovery, as opposed to their motivational state at the time of caching. Although being consistent with prospection abilities (Future Planning Hypothesis), this evidence could equally be interpreted through alternative explanations. In particular, the Compensatory Caching Hypothesis – which specifically challenges jays' apparent future planning behaviour in Raby et al. (2007)'s study – suggests that jays may 'have a propensity to cache a particular food type in a given location that differs from the foods that have been previously associated with that location, a strategy that would provide more uniform distribution of resources' (Shettleworth personal comm., as cited in Dickinson, 2011, page 90; see also Chapter 3 for more details). In Chapter 3 I reported a novel paradigm aimed at disambiguating whether jays' apparent caching for the future is underpinned by future panning abilities or by a natural predisposition to allocate caches evenly among different locations. Consistently across two experiments, jays did not cache as predicted by either hypotheses, thereby questioning both cognitive mechanisms proposed to account for jays' caching for the future.

In **Chapter 4**, I continued my multifaceted investigation of cognition in the Eurasian jay by focusing on the social domain. Building on previous reports that these jays can adjust their caching behaviour by responding to the visual perspective (Legg and Clayton, 2014) and current desire (Ostojić et al., 2017) of a competitor, I conducted two experiments aimed at testing whether the jays could respond to both social cues simultaneously to most effectively protect their caches. In Experiment 4.1, the jays could cache only one type of food – either the same food the observer was sated on or a different food – but could choose to distribute their caches across locations that were in-view and out-of-view for the observer. In Experiment 4.2, jays could hide food only in one location (either visible or not visible to the observer) but could choose between two types of cacheable foods: one that was currently desired and one that was not currently desired by the observer. In both experiments, I found no evidence that Eurasian jays can limit the risk of cache loss by integrating cues correlating with the visual perspective and current desire of another agent. Crucially, jays' performance was also inconsistent with previous literature: Eurasian jays did not employ cache protection strategies based on one of the two social cues alone. This result was surprising considering that in Experiment 4.2 and 4.3 I employed two paradigms that closely matched those used by Legg and Clayton (2014) and Ostojić et al. (2017) and which showed, respectively, that Eurasian jays responded to others' visual perspective and desire in the caching context.

In **Chapter 5**, I therefore decided to further investigate this unexpected outcome by assessing the reliability of the two original effects, independently. To this end, Experiment 5.1 was a direct replication of Legg and Clayton (2014)'s study. In contrast with the original study but in line with the outcome of Experiments 4.1, I found no evidence that Eurasian jays prefer to cache behind an opaque barrier when a conspecific is present relatively than when a conspecific is not present. In Experiment 5.2, I tested whether the inconsistencies between the results of Experiment 4.2 and Ostojić et al. (2017)'s study may have been caused by a minor difference in the set-up, namely the present/absence of a transparent barrier in proximity of caching tray. I found that jays' caching pattern was not affected by the slightly different set-ups, and crucially again that jays did not adjust their caching pattern by taking into account the current desire of another bird, thus further corroborating the results of Experiment 4.2. Taken together, the experiments reported in Chapters 5 and 4 appear to challenge the reliability and robustness of previous literature on Eurasian jays' social cognition.

7.1.2: IMPLICATIONS AND FUTURE DIRECTIONS

Overall, the four empirical studies reported in this thesis allow limited conclusions about whether the Eurasian jay is endowed with a flexible and domain general cognitive tool-kit. Consequently, my findings cannot support Emery and Clayton (2004)'s hypothesis that cognitive convergence between corvids and apes may extent to the third and deeper level of analysis (Seed, 2007).

With regard to physical problem solving, Experiment 2.3 demonstrated that Eurasian jays – as rooks (Bird and Emery, 2009) and New Caledonian crows (e.g.

Auersperg et al., 2011) – are capable of solving a task with a familiar apparatus by using objects that they were not previously trained to use as tools, namely sticks. The performances of the jays in the experiment also showed that they could employ an alternative strategy to solve the task. When provided with sticks, jays could collapse the internal platform of the apparatus by actively pushing the tool against it, a behaviour that differed from the one they had learned in the training, i.e. simply dropping a tool into the apparatus. Therefore, it seems likely that physical problem solving in the Eurasian jays may be underpinned by some degree of cognitive flexibility. On the other hand, Experiments 2.1 and 2.2 tentatively suggests that the tool selectivity abilities of the Eurasian jay may be less developed that those of fellow corvids, most notably the rook (Bird and Emery, 2009) and the New Caledonian crow (Chappell and Kacelnik, 2002; Jelbert et al., 2019; Knaebe et al., 2017), although a number of arguments impose this consideration to be taken with caution (see Chapter 2). Thus, when the outcomes of the three experiments reported in Chapter 2 are considered together, evidence cannot support the idea that Eurasian jays share comparable cognitive sophistication in the physical domain with members of the *Corvus* genus (e.g. rooks, New Caledonian crows). However, it will be crucial for future research to continue the investigation of physical problem solving in the Eurasian jay, particularly by presenting jays with paradigms that have been already used in other corvids. For instance, it will be extremely interesting to test whether, as rooks (Bird and Emery, 2009), Eurasian jays could modify objects (e.g. remove side branches from twigs) or shape raw materials (e.g. craft hook from straight wire) to obtain functional tools. This approach will ultimately allow a deeper understanding of the physical cognition of these jays, as well as fostering insights into whether the remarkable problem solving ability reported in the *Corvus* genus is a cognitive specialization of this group or rather a feature widely spread within the corvid family.

With regard to future planning and social cognition abilities, the findings reported in Chapters 3 to 5 limit solid conclusions on the cognitive flexibility of the Eurasian jay in these domains; yet, these findings appear to challenge previous literature. This is because jays' performance in Experiments 3.1 and 3.2 was not consistent with either of the two cognitive mechanisms that have been proposed to possibly underpin jays' caching for the future. In contrast, both alternative scenarios – i.e. data in line with either the Future Planning or the Compensatory Caching Hypothesis – would have represented a significant contribution to our understanding of the apparent prospection cognition in these jays. In a similar vein, Experiments 4.1 and 4.2 not only provided no indications that Eurasian jays can integrate another's visual perspective and current desire to limit cache loss but – together with the findings reported in Chapter 5 – also questioned jays' ability to respond to one of the two social cues independently, as reported by Legg and Clayton (2014) and Ostojić et al. (2017).

In the discussion sections of Chapters 3, 4 and 5 I put forward a number of thoughts that may help to interpret the negative finding of each study, and considered next steps for future research. In what follows, I will attempt to convey a more broad and systemic discussion about why three out of four of the empirical studies I conducted may have yielded outcomes inconsistent with previous literature.

In recent years, science has faced a 'replication crisis' (Baker, 2016). A number of studies across fields have attempted at replicating published results, finding that only a small proportion of the original effects could be replicated (e.g. medicine, Prinz et al., 2011; behavioural economics, Camerer et al., 2016; genetics, Munafò, 2009; neuroscience, Button et al., 2013). Psychology appears to be particularly challenged by the current crisis (Braver et al., 2014; Maxwell et al., 2015; Shrout and Rodgers, 2018). For instance, over 100 published studies in psychology, only in the 39% of cases results could be considered as successful replications (Open Science Collaboration, 2015). Science hinges on confirming evidence by replicating previous findings, so that this unexpected scenario is posing a serious challenge to the very credibility of research. In other words, the replication crisis is forcing scientists to ask themselves: how much of what we think to know is actually true? Further, how could science have produced such a large body of apparently unreliable lines of evidence? In the attempt of addressing these questions, a number of issues have been proposed as the factors that may have participated in producing high rates of spurious results. Some of these issues are systemic and apply to all scientific disciplines, for instance, unconscious biases of researchers (e.g. confirmation bias), journals' bias towards publishing positive results over negative findings, questionable research practice (e.g. p-hacking, stop data collection on the basis of interim analyses), 'blind' reliance and misuse of the null-hypothesis testing approach (Farrar and Clayton, 2019; Farrar and Ostojić, 2019; Ioannidis, 2005; Stevens, 2017). In addition, other issues can exacerbate the proportion of false positives in certain fields (Ioannidis, 2005). With regard to comparative cognition, a number of factors are likely to make this field particularly susceptible to false positive discoveries and in parallel, resilient at recognizing such spurious results through replication studies. First, the typical small sample sizes employed in comparative cognition increase the risk of false positives (Ioannidis, 2005) and decrease the chance of replicating previously reported effects (Stevens, 2017) due to underpowered statistical analyses. Second, similar effects are caused by a common focus on phenomena characterized by small effect size and noisy measurements, with the latter being, in some cases, aggravated by paradigms involving a single/few test trials and/or between-subjects designs (Farrar and Clayton, 2019; Farrar and Ostojić, 2019). Third, the repeated testing of the same individuals in multiple studies over years (or decades!) affects the replicability of findings because: i) it undermines the possibility of conducting truly independent replications; ii) specific experimental histories may alter individuals' performance in subsequent studies, and impair the collections of consistent results among different laboratories; iii) aging may affect cognitive performance of individuals over time (Farrar and Clayton, 2019; Farrar and Ostojić, 2019; Stevens, 2017). With this in mind, it is possible that the line of evidence constituting the theoretical and methodological foundations of this thesis may represent false positive findings. My future planning experiments (Chapter 3) built on two studies: Cheke and Clayton (2012)'s evidence that Eurasian jays cache according to future needs, and Raby et al. (2007)'s paradigm which inspired the design of Experiments 3.1 and 3.2 because it provided evidence in line with both the Future Planning and Compensatory Caching Hypotheses in California scrub-jays. My social cognition experiments (Chapter 4, 5) also stemmed from two previous studies, namely Legg and Clayton (2014) and Ostojić et al. (2017) that showed, respectively, that Eurasian jays respond to others' visual perspective and desire in the caching context. These four studies bear some of the key issues fostering the chance of false positive findings in comparative cognition, such as small sample size, which range from n=4 in Cheke and Clayton (2012) to n=16 in Ostojić et al. (2017), and protocols involving only a single/few test trials. Further, no follow-up experiment that confirmed/contradicted the effects reported in these four studies – or the effectiveness of the paradigm in the case of Raby et al. (2007) – was published prior to this thesis. For instance, in contrast to the ability to attribute desires in the food-sharing context which was detected in multiple studies (Ostojić et al., 2013, 2014, 2016), Ostojić et al. (2017)'s experiment represents the only evidence that Eurasian jays (or corvids in general) may be capable of taking into account the current desire of a competitor to protect their caches. Therefore, it is possible that some of these studies may have yielded spurious effects. Crucially however, the experiments I have conducted are not exempt from similar concerns. For instance, having access to a limited number of Eurasian jays – as typical in comparative cognition – my studies were also characterized by limited sample sizes. The protocols employed were also constrained by the number of testing trials, most notably Experiment 3.1 and 3.2 – like Raby et al. (2007) – involved a single test trial, to prevent jays' performance from being affected by learning process. Consequently, it cannot either be excluded that my data resulted in underpowered statistical analyses, which may have led to false negatives. Additionally, given that all individuals tested in Chapters 3 to 5 were born in 2006/8 and participated in a number of future planning and social cognition studies through their lives, it is also possible that their experimental histories or age may have fostered contrasting results in my studies and the previous literature (see also Chapter 5).

Overall, these considerations cannot shed light on whether the inconsistencies between the studies I have conducted here and the previous literature are due to false positives in the former or in the latter case. However, the points raised above have fundamental implications for framing my findings into a wider picture and crucially, for recognizing objectives for future research.

In my view, it is essential for comparative psychologists to consider taking one step sideways and attempt at evaluating the robustness and reliability of what has been envisioned as 'established' phenomena, before to rush toward the search of more complex and ground-breaking effects. With the regard to the study of convergent cognition in corvids, this approach could translate into a careful re-evaluation of the hypothesis of a second-level convergence through the systematic re-assessment of the evidence available. A series of tools can allow to attain this goal, including critical re-analysis of reported effects (Farrar and Clayton, 2019), replications of published studies and simulations. Additionally, meta-analyses can also play a key role (Braver et al., 2014; Maxwell et al., 2015). For instance, recent meta-analyses of water displacement experiments in New Caledonian crows, rooks, Eurasian jays and California scrub-jays indicated that corvids' performance in these studies may have been underpinned *only* by simple learning and/or initial predispositions, thus challenging the original interpretations that some level of causal understanding may have guided the birds' behaviour (Ghirlanda and Lind, 2017; Hennefield et al., 2018).

Ultimately, as corvids researchers, cognitive psychologists or simply scientists, we should embrace the idea that science is a slow and stepwise process. Without verifying the reliability of the evidence available we will take the risk that next generation researchers may build their research questions on spurious effects, thereby forcing science in vicious circle.

7.2: CEPHALOPODS

7.2.1: SUMMARY OF RESULTS

To address the second objective of my thesis, in **Chapter 6** I endeavoured at laying theoretical and methodological groundwork for the study of cognitive convergence between cephalopods and large-brained vertebrates. In the first part of the chapter I reviewed the most compelling instances of behavioural flexibility in octopus, cuttlefish and squid, and building on this, I proposed that current evidence may be sufficient to hypothesize a case of behavioural convergence (first-level convergence) among these groups. Subsequently, in the second part of the chapter, I discussed the process that may have led to the evolution of large brains and behavioural flexibility in cephalopods. I suggested that a first key step in this process may have occurred together with the modification of the protective shell into a buoyance device; yet the major cognitive leap may have followed the internalization/loss of the shell in the ancestors of coleoids. This is because the disappearance of the external shells may have produced a dramatic increase in unavoidable mortality and facilitated widespread colonization of complex niches, thus in turn selecting fast life histories and driving cephalopods to cope with novel challenges. Cephalopods' cognitive sophistication might have emerged primarily in response to predation and complex feeding contexts but social challenges, particularly during mating, might have acted as additional selective pressures. Finally, in the last part of the chapter, I described novel paradigms that could allow to explore cognitive convergence between cephalopods and large-brained vertebrates at a deeper level by providing baseline data of the cognitive flexibility of the octopus in the physical, prospection and social domains.

7.2.2: IMPLICATIONS AND FUTURE DIRECTIONS

My analysis tentatively suggests that cephalopods and large-brained vertebrates may have evolved cognitive sophistication through a partially different process, namely in response to different sets of evolutionary pressures and together with divergent life histories. If supported by empirical evidence, this hypothesis will have fundamental implications for our understanding of the evolution of intelligence.

With regard to the factors triggering the evolution of intelligence, evidence in primates, corvids and other groups of large-brained vertebrates indicates that challenging foraging niches (Ecological Intelligence Hypothesis, Rosati, 2017) and complex social environments (Social Intelligence Hypothesis, Byrne, 2018; Whiten, 2018) are the key drivers (see also Chapters 1 and 6). Cephalopods may question this view (Amodio et al., 2019b, 2019a). On the one hand, the problems faced by cephalopods in finding and processing food appear comparable to those experienced by large-brained vertebrates (e.g. reliance on extractive foraging, ephemeral resources, generalist diets), thus indicating that the complexity of foraging niches may have participated in selecting for higher cognitive power also in these molluscs. On the other hand, cephalopods are not known for engaging in complex and enduring social bods (Boal, 1996; Hanlon and Messenger, 2018; Schnell and Clayton, 2019), so that the Social Intelligence Hypothesis may not be applicable to this group. Yet alternative selective pressures may have participated in shaping cognitive evolution in cephalopods. In particular, I proposed that high predatory pressures – resulting from the disappearance of the external shell – may have represented a major drive in cephalopods cognitive evolution, thus extending the classic view of this factor as a trigger for sophisticated behavioural and physiological adaptations (e.g. dynamic skins; Hanlon and Messenger, 2018; Packard, 1972). Empirical support for the hypothesis that intelligence may evolve as a cognitive adaptation to cope with the challenges of predator–prey interactions has been found in fish (van der Bijl et al., 2015; van der Bijl and Kolm, 2016), carnivores and herbivores (Jerison, 1973; Köhler and Moyà-Solà, 2004). Further, from the opposite perspective, the recent finding that morphological defence structures (e.g. spines in hedgehogs, dermal plates in armadillos) co-evolved with reduced encephalization quotients in mammals provides additional support to this hypothesis because it corroborates the idea that effective anti-predator adaptations may relax the cognitive challenges posed by predators (Stankowich and Romero, 2017).

I also hypothesized that cognitive sophistication may also have emerged in response to challenging reproductive scenarios: cephalopods need to employ flexible mating strategies to reduce the risk of being cannibalized and to maximize their reproductive efforts within a single, short interval (see also Schnell and Clayton, 2019). In other words, a different kind of social problems may have shaped cognitive evolution in cephalopods, relatively to primates, in which the challenges of competing and cooperating with multiple groups members are considered the key social driver (Dunbar, 1992; Dunbar and Shultz, 2007; Kudo and Dunbar, 2001), or corvids, in which the need to maintaining a life-long monogamous bond with their mate may have played an equivalent role (Emery et al., 2007). A recent study in Squamata (lizards and snakes) supports the idea that different factors may account for variability in cognitive sophistication among different group. De Meester et al. (2019) found no correlation between that brain size and either habitat or social complexity within Squamata, thus raising the possibility that alternative pressures may account for the variability in cognitive complexity among lizards and snakes.

With regard to the co-evolution of intelligence and slow life history, evidence from birds and mammals consistently support the existence of tight link between these factors (Gonzales-Lagos et al., 2010; Minias and Podlaszczuk, 2017; Street et al., 2017; Wirthlin et al., 2018). Yet, given their fast life histories, cephalopods pose a challenge to the idea that intelligence must coevolve with slow life history, thereby questioning the hypotheses that a slow development is necessary to overcome the costs of a large brain and/or a consequence of the reduced extrinsic mortality resulting from enhanced cognition (Barton and Capellini, 2011; Sol, 2009a). Interestingly, a recent simulation study showed that short life spans can select for cognitive complexity (i.e. learning speed), thus providing preliminary support to this view (Liedtke and Fromhage, 2019).

Cephalopods' cognitive evolution may inspire new angles in the study of large-brained vertebrates. For instance, the role played by predation in the evolution of intelligence has been discussed in primates (Byrne and Bates, 2007; Zuberbühler and Jenny, 2002), yet it received substantially less attention in this group or in other large-brained vertebrates. In this thesis I have hypothesized that predation risk may have acted as key trigger for the emergence of complex sophistication in cephalopods. It is possible that this factor may also have had a significant impact on the evolution of large-brained vertebrates, both directly and indirectly (van der Bijl and Kolm, 2016). Dunbar and Schultz (Dunbar and Shultz, 2017), suggest that predation was the main driver for group size in primates. Larger groups then created a demand for enhanced cognitive complexity to cope with the more challenging social environment, thus favouring ecological intelligence to meet the energetic demands of larger brains. If this was the case then in contrast to cephalopods, predation might have represented an *indirect* driver for the emergence of intelligence at the initial stage. In addition to group living, other anti-predator adaptations such as arboreality, large body size and flight might have reduced extrinsic mortality in apes, cetaceans, elephants, corvids, and parrots (Healy et al., 2014), thus favouring the co-evolution of slow life histories and intelligence. Subsequently, key features of slow life histories, such as high investment in a limited number of offspring and long periods of dependency might have resulted in higher demands for cognitively complex anti-predator strategies. Since young dependent offspring are subject to higher predation rates (Connor, 2007; e.g. due to weaker motor coordination, smaller size, less experience) than adults, there might be strong selection pressure on the parents' intelligence to protect offspring from predators. Such selection pressure can explain, for instance, the emergence of complex group coordination in cetaceans to fight against predatory assaults on calves (Connor, 2007). Thus, at a later stage, predation on offspring might have acted as direct pressure for the evolution of intelligence in large-brained vertebrates. If so, predation might have favoured the evolution of both cognitive (e.g. intelligence) and non-cognitive (e.g. life history) adaptations in large-brained vertebrates and in cephalopods - albeit through different evolutionary pathways. It must also be noted that adult apes, cetaceans, corvids, and parrots are not exempt from lethal aggression from predators. Thus, it cannot be excluded that predatory pressures in adulthood also participate in shaping their cognition. Supporting this idea, complex communication systems allowing the signalling of distinct kinds of predators have evolved in arboreal primates (Seyfarth et al., 1980). Furthermore, it has been recently shown that crows can identify new predators according to their proximity to dead conspecifics (Swift and Marzluff, 2015) and other corvids avoid areas in which a dead conspecific was spotted and actively share this information with other individuals (Iglesias et al., 2012). Hence, it is possible that predation risk on adults might also have participated in selecting intelligence in large-brained vertebrates. Future research may investigate whether predatory pressure acted only as an indirect trigger, for instance, by favouring the arising of novel socio-ecological challenges, or whether it also played a direct role in selecting for enhanced intelligence. Furthermore, it may also be interesting to test the cognitive underpinnings of antipredatory strategies in large-brained vertebrates, particularly those involving the defence of offspring.

All things considered, cephalopods' cognitive evolution has the potential to impose a reappraisal of the factors fostering the emergence of intelligence, thereby raising the possibility that cognitive sophistication is not constrained to a single evolutionary route. Therefore, the theoretical analysis reported in Chapter 6 together with the points raised above strongly support the notion that cephalopods as a promising novel model group for the study of convergence cognitive evolution.

Nonetheless, further research will be essential to widen our understanding of the cognitive evolution of this groups. In particular, there are two fundamental approaches that should be pursued. On the one hand, correlational analyses should be conducted to test the relative influence ecological, predatory, and social pressures in the evolution of cephalopods' cognition. For instance, morphological and behavioural proxies for intelligence could be measured in species that are subject to different levels of predation (e.g., density and number of predator species) in order to investigate the influence of predation in the evolution of intelligence. Given the remarkably large geographic range of some species (e.g. common octopus, Jerep et al., 2014), correlational analyses could also focus on within-species differences, an approach recently employed in birds (Ashton et al., 2018). On the other hand, it will be equally important to pursue a parallel line of research aimed at assessing the cognitive underpinning cephalopods' behavioural flexibility. This approach will ultimately lead to gain insight into whether cephalopods can perform cognitive process more complex than hardwired predispositions and simple learning, and thus to evaluate the hypothesis of a second-level convergence between these molluscs and large-brained vertebrates.

Testing cephalopods' cognition will pose challenges. For instance, tasks and apparatuses devised for primates or birds are unlikely to be directly applicable to cephalopods, due to the dramatic difference in in morphology and perception. Consequently, researchers must dedicate efforts to modify or design tasks *ad hoc* for these animals. However, the use of cephalopods as a model may also carry benefits, such to relieve some of the endemic issues fuelling unreliable findings in comparative cognition. For instance, the long and repeated testing of the same individuals for multiple studies/years is not a concern for cephalopods research because of their short-life spans. Further, cephalopods research can, in most cases, sustain larger sample size than equivalent research on primates, corvids, cetaceans, or elephants. Cephalopods laboratories typically acquire specimens from the wild and following data collection, euthanize or release them back into the sea, depending on the purpose of the study. It is therefore achievable for a single laboratory with limited housing facilities, to obtain sample size larger than the average for comparative cognition (e.g. tens of individuals) by testing multiple stocks of individuals in sequence. Such a strategy would not only raise limited ethical concerns, but also keep the costs of husbandry low because for behavioural investigations specimens may be released back to the wild at the end of the study.

7.3: CONCLUDING REMARKS

Taken together, my empirical research in Eurasian jays challenges Emery and Clayton (2004)'s hypothesis that corvids evolved – convergently with apes – a flexible and domain-general cognitive tool kit. Although I showed that the Eurasian jay is capable of some level of flexibility in using tools, my results indicated limited tool selectivity abilities in this species and my findings in other domains were inconsistent with previous studies reporting sophisticated abilities in planning for the future and in solving social problems. The lack of consistency between previous literature and the present thesis may have resulted either from false positives in the former or false negatives in the latter. In parallel, my research on cephalopods strongly suggested that these molluscs are an intriguing new model group for studying convergent cognitive evolution, and laid theoretical and methodological groundwork for this purpose.

Overall, the present thesis represented a step forward in understanding the cognitive evolution of corvids and cephalopods. However, future research will be essential to acquire deeper insights into this topic. With regards to corvids, I contended that a key goal will be to re-evaluate the hypothesis of a second-level convergence between these large-brained birds and apes. This could be achieved by using a multifaceted approach (e.g. replications, meta-analyses, simulations) to assess the reliability of the evidence in support of cognitive sophistication in corvids.

With regards to cephalopods, the systematic investigation of complex cognition in different domains will be vital to test whether the behavioural convergence between these molluscs and large-brained vertebrates extends to cognitive similarities. Ultimately, a further focus on corvids and cephalopods can shed light on fundamental aspects of the convergent evolution of cognition.

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APPENDIX A:

BIRD DATA

Table A1: Individual jays data. Number in round brackets indicate an experiment in which the bird acted *only* as observer of the focal bird. Number in square brackets indicate an experiment in which the bird was either unable to complete testing or was excluded from the analysis based on pre-determined criteria. Note that Jerusalem was euthanized out of welfare reasons (unrelated to the testing) before the start of Experiments 3.2, 5.1, 5.2.

Colony	Bird	Sex	Born	Experiment
1	Caracas	M	May 2006	3.1; 3.2; 4.1; 4.2; 5.1; 5.2
1	Dublin	M	May 2006	[3.1]; [3.2]; [4.2]; 5.1; 5.2
1	Jerusalem	F	May 2006	3.1; 4.1; 4.2
1	Lima	M	May 2006	[3.1]; [3.2]; 4.1; 4.2; 5.1; 5.2
1	Lisbon	M	May 2006	3.1; 3.2; (4.1); [4.2]; 5.1; [5.2]
1	Quito	F	May 2006	3.1; 3.2; 4.1; 4.2; 5.1; 5.2
1	Rome	F	May 2006	[3.1]; 3.2; 4.1; 4.2; 5.1; 5.2
1	Washington	F	May 2006	3.1; 3.2; 4.1; 4.2; 5.1; 5.2
1	Wellington	F	May 2006	3.1; 3.2; 4.1; 4.2; 5.1; 5.2
2	Hunter	F	May 2008	5.1
2	Adlington	F	May 2008	(5.1)
3	Chinook	F	May 2015	2.1a
3	Homer	M	May 2015	2.1; 2.2; 2.3
3	Jaylo	F	May 2015	2.1; 2.2; 2.3
3	Stuka	F	May 2015	2.1; 2.2; 2.3
3	Poe	M	May 2015	2.1; 2.2; 2.3

APPENDIX B:

TEST DATA

CHAPTER 2:

All test data are available at https://doi.org/10.5281/zenodo.3471706.

CHAPTER 3:

All test data are available in Tabs. 3.1 and 3.2 (see Chapter 3)

CHAPTER 4:

Table B1: Test data of Experiment 4.1. 'Barrier Orientation' denotes the orientation of the barrier within the cacher's compartments: 'out-in' means that opaque arm of the T-barrier was facing the out-door aviary and the clear arm of the T-barrier was facing the door of the testing compartment; 'in-out' corresponds to the opposite orientation. The 'Prefeeding' columns denote the kind of food and the number of items taken out of the bowl by the observer bird in the prefeeding phase. 'IV' (in-view) and 'OV'(out-of-view) denote, the number of items cached in (or retrieved from) the tray placed behind the clear arm and the opaque arm of the T-barrier respectively. 'P' and 'M' refer to peanuts and Macadamia nuts respectively. Yellow cells denote the trials that were repeated because no item was cached.

				Prefeeding Observer		Caching			Recovery			
									Retrieved		Recached	
Bird	Observer	Barrier Orientation	Trial	Food	Taken	Food	IV	OV	IV	OV	IV	OV
Caracas	Lisbon	out-in	1	M	6	M	8	8	1	0	0	0
			2	P	6.5	M	4	0	4	n/a	0	n/a
Lima	Lisbon	in-out	1	P	11	P	0	0	n/a	n/a	n/a	n/a
			2	M	2	P	0	0	n/a	n/a	n/a	n/a
	Wellington		1 Rep.	P	10.5	P	0.5	0	0	n/a	0.5	n/a
			1 Rep.	M	0	P	0.5	0	0.5	n/a	0	n/a
Rome	Caracas	out-in	1	M	6	P	5	1	0	0	1	0
			2	P	7	P	0	1	n/a	0	n/a	0
Jerusalem	Caracas	out-in	1	P	13	P	3	0	2	n/a	0	n/a
			2	M	1	P	6	1	5	0	0	0
Wellington	Rome	in-out	1	P	0	M	6	4	0	0	0	0
			2	M	4	M	5	6	0	0	0	0
Quito	Caracas	in-out	1	M	1	P	13	17	0	0	0	0
			2	P	0	P	0	7	n/a	0	n/a	0
Washington	Jerusalem	out-in	1	P	10	M	3	8	0	0	0	0
			2	M	0	M	6	4	0	0	0	0

Table B2: Test data of Experiment 4.2. The 'Prefeeding' columns denote the kind of food and the number of items taken out of the bowl by the observer bird in the prefeeding phase. The 'Barrier' column denotes the U-barrier used in the trial (clear, 'C'; opaque, 'O'). 'P' and 'M' refer to peanuts and Macadamia nuts respectively. Yellow cells denote the trials that were repeated because no item was cached. Note that in the case of Jerusalem' trial 4, the same trial was repeated twice.

			Pre-Feeding		**Caching**					**Recovery**			
			Observer			**Taken**		**Cached**		**Recovered**		**Recached**	
Cacher	**Observer**	**Trial**	**Food**	**Taken**	**Barrier**	**P**	**M**	**P**	**M**	**P**	**M**	**P**	**M**
Caracas	Rome	1	M	2	C	27	12	22	9	0	0	0	0
		2	P	2	C	31	1	28,5	1	0	0	0	0
		3	M	1	O	29	0	24	0	0	na	0	na
		4	P	1	O	10	0	8	0	0	na	0	na
Wellington	Rome	1	M	1	O	2	1	1	0	1	na	0	na
		2	P	1	O	0	2	0	1	na	0	na	0
		3	M	3	C	3	4	1	1	1	1	0	0
		4	P	2	C	1	6	0	4	na	2	na	0
Jerusalem	Caracas	1	P	14,5	C	6	8	1	2	0	0	0	0
		2	M	2	C	12,5	0	3	0	0	na	1,5	na
		3	P	7	O	9	12	0	1	na	1	na	0
		4	M	1	O	11	0	0	0	na	na	na	na
		4 Rep. 1	M	1	O	10	10	0	0	na	na	na	na
		4 Rep.2	M	2	O	3	15	0	1	na	1	na	na
Quito	Caracas	1	P	4	O	1	4	1	2	0	0	0	0
		2	M	3	O	1	16	1	15	0	0	0	0
		3	P	5	C	5	2	5	1	0	0	0	0
		4	M	2	C	3	3	3	1	0	0	0	0
Lima	Wellington	1	M	6	C	8,5	14	1,5	6	1	1	0	0
		2	P	6,5	C	13,5	1	0	0	na	na	na	na
		3	P	3	O	10	8	3	0	2	na	0	na
		4	M	4	O	2	13	0	0	na	na	na	na
		2 Rep.	P	1	C	11,5	2	2	0	2	na	0	na
		4 Rep.	M	2	O	15	10	3,5	0	2,5	na	0	na
Washington	Jerusalem	1	P	11	O	6,5	8	0	4	na	2	na	0
		2	M	5	O	3	8	0	5	na	1	na	1
		3	M	5	C	5	4	1	2	1	2	0	0
		4	P	7	C	2	8	0	3	na	0	na	0
Rome	Washington	1	M	3	O	0	1	0	0	na	na	na	na
		2	P	9	O	0	4	0	2	na	0	na	0
		3	P	5	C	0	3	0	3	na	0	na	0
		4	M	8	C	0	3	0	2	na	0	na	0
		1 Rep.	M	12	O	0	6	0	5	na	0	na	0

Appendix B

Table B3: Test data of Experiment 5.1. 'Barrier Orientation' denotes the orientation of the barrier within the cacher's compartments: 'out-in' means that opaque arm of the T-barrier was facing the out-door aviary and the clear arm of the T-barrier was facing the door of the testing compartment; 'in-out' corresponds to the opposite orientation. 'IV' (in-view) and 'OV'(out-of-view) denote, the number of items cached in (or retrieved from) the tray placed behind the clear arm and the opaque arm of the T-barrier respectively. 'P', 'S' and 'D' ('Condition' column) refer to the *Private, Observed by Subordinate*, and *Observed by Dominant* condition respectively. Yellow cells denote Dublin's trial 2 which was repeated with a different individual as dominant observer, due to the unusual behaviour by the pre-planned observer, Rome (see Chapter 5 for details).

					Caching		**Recovery**			
							Retrieved		**Recached**	
Bird	**Trial**	**Condition**	**Observer**	**Barrier Orientation**	**OV**	**IV**	**OV**	**IV**	**OV**	**IV**
Caracas	1	P	na	out-in	2	2	0	0	0	0
	2	S	Washington	out-in	3	2	0	0	0	0
	3	S	Washington	in-out	0	4	na	0	na	0
	4	P	na	in-out	3	5	0	0	0	0
Washington	1	D	Caracas	out-in	1	1	0	0	0	0
	2	P	na	out-in	2	1	1	0	1	1
	3	D	Caracas	in-out	1	1	1	0	0	0
	4	P	na	in-out	2	3	0	0	0	0
Lisbon	1	D	Caracas	in-out	0	0	na	na	na	na
	2	P	na	in-out	0	0	na	na	na	na
	3	S	Washington	in-out	1	3	0	0	0	0
	4	P	na	out-in	0	0	na	na	na	na
	5	D	Caracas	out-in	0	0	na	na	na	na
	6	S	Washington	out-in	10	7	0	0	0	0
Quito	1	P	na	in-out	0	1	na	0	na	0
	2	S	Washington	in-out	1	2	0	0	0	0
	3	D	Caracas	in-out	1	1	0	0	0	0
	4	S	Washington	out-in	2	0	0	na	0	na
	5	P	na	out-in	0	2	na	0	na	0
	6	D	Caracas	out-in	1	0	0	na	0	na
Rome	1	S	Quito	out-in	0	0	na	na	na	na
	2	D	Caracas	out-in	0	0	na	na	na	na
	3	P	na	out-in	1	0	0	na	0	na
	4	D	Caracas	in-out	0	0	na	na	na	na
	5	P	na	in-out	0	0	na	na	na	na
	6	S	Quito	in-out	0	2	na	0	na	0
Wellington	1	D	Lisbon	out-in	0	0	na	na	na	na
	2	S	Quito	out-in	0	0	na	na	na	na
	3	P	na	out-in	1	2	0	0	1	2
	4	S	Quito	in-out	0	0	na	na	na	na
	5	D	Lisbon	in-out	0	1	na	1	na	0
	6	P	na	in-out	0	0	na	na	na	na
Dublin	1	P	na	in-out	2	4	0	0	1	1
	2	D	Rome	in-out	0	0	na	na	na	na
	3	S	Washington	in-out	0	0	na	na	na	na
	4	S	Washington	out-in	0	0	na	na	na	na
	5	P	na	out-in	0	0	na	na	na	na
	6	D	Caracas	out-in	0	0	na	na	na	na
	2 Repl	D	Caracas	in-out	0	0	na	na	na	na
Lima	1	S	Wellington	in-out	11	11	1	11	0	0
	2	D	Caracas	in-out	0	0	na	na	na	na
	3	P	na	in-out	3	13	0	12	0	0
	4	P	na	out-in	0	0	na	na	na	na
	5	D	Caracas	out-in	0	0	na	na	na	na
	6	S	Wellington	out-in	0	0	na	na	na	na
Hunter	1	P	na	in-out	0	0	na	na	na	na
	2	S	Adlington	in-out	1	0	0	na	na	na
	3	S	Adlington	out-in	0	0	na	na	na	na
	4	P	na	out-in	2,5	1	0	0	0	0

Table B3: Test data of Experiment 5.2. The 'Prefeeding' columns denote the kind of food and the number of items taken out of the bowl by the observer bird in the prefeeding phase. The 'Barrier' column denotes whether the clear U-barrier was used in the trial (Barrier, 'B') or no barrier was used in the trial (No barrier, 'N'). 'P' and 'M' refer to peanuts and Macadamia nuts respectively. Yellow cells denote the trials that were repeated because no item was cached. Note that Lisbon consistently cached no item in trials 1-3 (blue cells), thereby this individual did not receive trial 4 (see Chapter 5 for details regarding the criteria for stopping data collection).

			Prefeeding			**Caching**				**Recovery**			
			Observer			**Taken**		**Cached**		**Retrieved**		**Recached**	
Cacher	**Observer**	**Trial**	**Food**	**Taken**	**Barrier**	**P**	**M**	**P**	**M**	**P**	**M**	**P**	**M**
Quito	Rome	1	M	2	B	7	7	5	4	0	0	0	0
		2	P	4	N	0	0	0	0	na	na	na	na
		3	M	2	N	7	2	4	1	0	0	0	0
		4	P	3	N	2	14	1	5	0	0	0	0
		2 Rep.	P	5	B	4	9	2	7	0	0	0	0
Wellington	Lima	1	P	14	B	0	16	0	1	na	0	na	0
		2	M	20	B	0	12	0	0	na	na	na	na
		3	P	24	N	0	7	0	0	na	na	na	na
		4	M	20	N	0	13	0	1	na	1	na	0
		2 Rep. 1	M	21	B	0	11	0	0	na	na	na	na
		3 Rep.	P	19	N	2	13	1	2	1	2	0	0
		2 Rep. 2	M	24	B	0	6	0	1	0	na	1	na
Lisbon	Dublin	1	M	7	N	4	2	0	0	na	na	na	na
		2	P	17	N	0	4	0	0	na	na	na	na
		3	M	2	B	6	5	0	0	na	na	na	na
Dublin	Lisbon	1	P	17	N	4	0	2	0	1	na	1	na
		2	M	9	N	18	0	10	0	2	na	0	na
		3	P	8	B	14	1	4	0	2	na	1?	na
		4	M	3	B	13	0	4	0	3	na	0	na
Caracas	Rome	1	M	3	B	11	26	9,5	26	0	2	0	0
		2	P	2	B	20	10	16	9	0	0	0	0
		3	M	4	N	7	36	6	32	0	0	0	0
		4	P	1	N	6	28	3,5	26	0	0	0	0
Rome	Wellington	1	P	4	B	0	11	0	9	na	0	na	0
		2	M	12	B	0	6	0	5	na	0	na	0
		3	P	5	N	0	7	0	6	na	0	na	0
		4	M	6	N	0	7	0	6	na	0	na	0
Lima	Dublin	1	M	0	N	20	12	7,5	0	5,5	na	1	na
		2	P	14	N	12	13	0,5	7	0	5	0,5	0
		3	M	0	B	12,5	12	1	9	0	1	0	0
		4	P	5	B	14,5	17	0,5	8	0	6	0	0
Washington	Lima	1	P	21,5	N	4	6	0	3	na	0	na	1
		2	M	11	N	4	7	2	6	1	2	0	0
		3	P	21,5	B	2,5	9	1	5	0	2	0	0
		4	M	17	B	6	10	0	6	na	2	na	1

APPENDIX C:

STATISTICAL ANALYSIS OF EXPERIMENTS 3.1 AND 3.2

ANALISYS

To determine the factors that best explain the caching behaviour, the number of items n_{bfc} of food type (*f*) cached by bird (*b*) in compartment (*c*) were treated as random variables drawn from Multinomial distributions with 7 or 4 categories – 2 × 3 for each food–compartment combination in Experiment 3.1, and 3 for each compartment in Experiment 3.2, respectively, plus one for not caching anything – and a uniform prior over 25 to 55 caching trials in total. Given the 15 minutes duration of the whole test trial, 25 trials correspond to an average time of 36 seconds per caching trial and 55 trials corresponds to 16 seconds per trial, during which each bird may decide to not cache anything or cache one item of the two food types in one of the three compartments. 8 and 6 different possibilities (models) were compared to set the rates r_{bfc} of the Multinomial distributions for Experiment 3.1 and 3.2, respectively. Models with rates independent of the food type are characterized by equal rates $r_{bf_1c} = r_{bf_2c}$ for both food types, whereas in models with food type dependent rates both r_{bf_1c} and r_{bf_2c} are treated as independent parameters. Similarly, models with rates independent of the bird identity have equal rates for all birds $r_{b_1fc} = r_{b_2fc} = \dots = r_{b_6fc}$ and models with rates independent of the compartment have equal rates for all 3 compartments $r_{bfc_1} = r_{bfc_2} = r_{bfc_3}$. Each model is characterised by the triple (food type dependence, bird identity dependence, compartment dependence), yielding $8 = 2^3$ different models for experiment 3.1 and a triple (bird identity dependence, compartment dependence, condition dependence), yielding $6 = 2^3 - 2$ different models for Experiment 3.2, where the subtraction of 2 is due to a between-group design regarding the condition of the bird, i.e. each bird was only tested on one condition. Uniform conjugate priors were used for the Bayesian model comparison. More explicitly, it is assumed that the probability of observing the actual counts n_{bfc} are given by:

$$P(n_{:::}|r_{:::}) = MULTINOMINAL\ (n_{:::}; r_{:::}) = \prod_{b} \frac{\left(\sum_{fc} n_{bfc}\right)!}{\prod_{fc} n_{bfc}\,!} \prod_{fc} r_{bfc}^{n_{bfc}}$$

(Equation 1)

where colons indicate index ranges, e.g. $n_{:::} = \left\{n_{b_1 f_1 c_1}, n_{b_1 f_1 c_2}, n_{b_1 f_1 c_3}, n_{b_1 f_2 c_1}, \cdots, n_{b_{D_b} f_{D_f} c_{D_c}}\right\}$, where D_b, D_f and D_c are the numbers of birds, food types and compartments, respectively. If the rates are independent of the food type, i.e. $r_{bc} = r_{bf_1c} = \cdots = r_{bf_{D_f}c}$, it is possible to rewrite Equation 1 to obtain:

$$P(n_{:::}|r_{:::}) = \prod_{b} \left[\prod_{c} \underbrace{\frac{\left(\sum_{f} n_{bfc}\right)!}{\prod_{f} n_{bfc}\,!} \prod_{f} \left(\frac{1}{D_f}\right)^{n_{bfc}}}_{UNIFORM-MULTINOMIAL\ (n_{b:c})} \right] \underbrace{\frac{\left(\sum_{fc} n_{bfc}\right)!}{\prod_{c}\left(\sum_{f} n_{bfc}\right)!} \prod_{c} \left(D_f r_{bc}\right)^{\sum_f n_{bfc}}}_{MULTINOMIAL\ (\sum_f n_{bf:}; D_f r_{b:})}$$

(Equation 2)

Note that $\Sigma_c D_f r_{bc} = \Sigma_{fc} r_{bfc} = 1$. Equation 2 has the natural interpretation of a hierarchical data generation process: First, sample the number of cached items per birds and compartment $\Sigma_f n_{bfc}$ according to rates $D_f r_{bc}$, second, sample for each bird and compartment the different food types from a uniform multinomial distribution (binomial in the case of only two food types).

Extra care should be given to the case, where the rates are independent of the bird, e.g. $r_{fc} = r_{b_1 fc} = \cdots = r_{b_{D_b} fc}$. In this case, it is possible to rewrite Equation 1 to obtain:

$$P(n_{:::}|r_{:::}) = \left(\prod_b \frac{\left(\sum_{fc} n_{bfc}\right)!}{\prod_{fc} n_{bfc}\,!}\right)\frac{1}{Z} \quad \underbrace{Z\prod_{fc} r_{fc}^{\sum_b n_{bfc}}}_{MULTINOMIAL\ (\sum_b n_{b::};r_{::})}$$

(Equation 3)

where $Z = \frac{(\Sigma_{bfc} n_{bfc})\,!}{\Pi_{fc}(\Sigma_b n_{bfc})\,!}$. Combining the rewritings of Equation 2 and Equation 3 allows to treat all other cases.

For the Bayesian model comparison, the posterior $P\ (n_{:::}|model) = \int dr_{:::} P(n_{:::}|r_{:::})\ P(r_{:::}|model)$ is obtained by integrating out the parameters weighted by a flat Dirichlet prior $P(r_{:::}|model)$ with parameter α = 1.

RESULTS AND INTERPRETATION

In Experiment 3.1, the Bayesian model comparison revealed that a model in which the caching rate depends on the identity of the bird and the type of food but not on the compartment is supported by the data better than any model in which the caching rate depends on the compartment (Fig. C1). Therefore, the overall pattern of results do not provide support for either the Compensatory Caching Hypothesis or the Mental Time Travel Hypothesis.

In Experiment 3.2, the Bayesian model comparison revealed that models with equal caching rates for all compartments have higher support than models with compartment-specific caching rates (Fig. C1), thus corroborating the results obtained in Experiment 3.1.

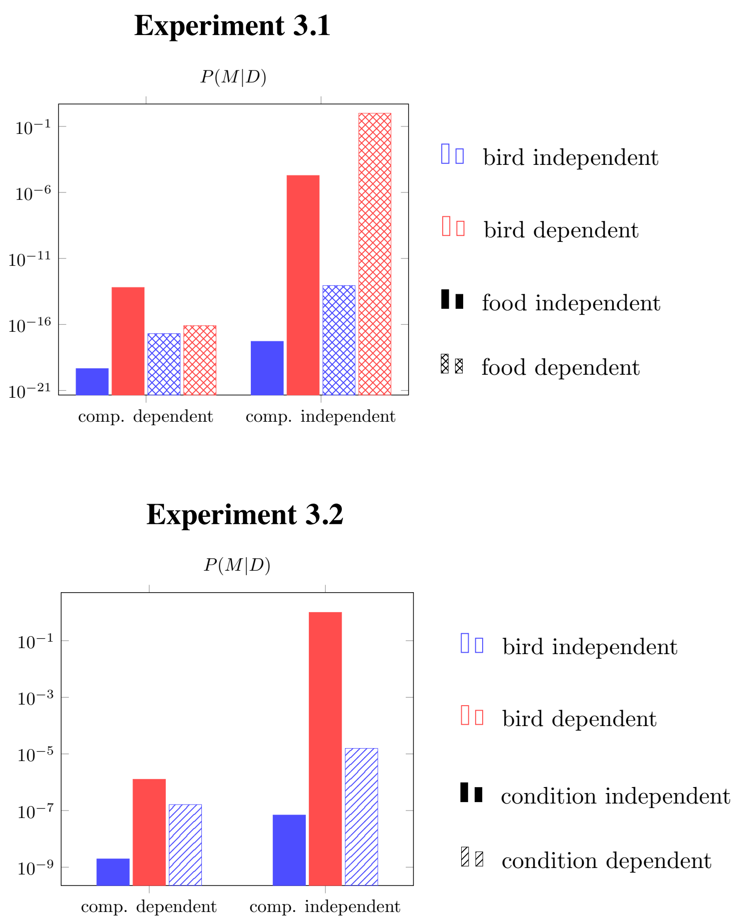

Figure C1: Bayesian model comparison. In Experiment 3.1 (top) the data is best explained by a model where the caching rate depends on the bird identity and the food type but not on the compartment, i.e. red crosshatch bar in the compartment independent group. In Experiment 3.2 (bottom), the data is best explained by a model where the caching rate depends on the bird identity but not on the compartment, i.e. solid red bar in the compartment independent group.

In sum, across both experiments the model with the best fit to the data was dependent on the identity of the bird and, in Experiment 3.1, the type of food cached. This means that birds seem to have cached predominantly their preferred food across the different locations regardless of their previous experiences in those locations.