

Relationship Quality and Cognition in Orange-Winged Amazons (*Amazona
amazonica*) and Blue and Gold Macaws (*Ara ararauna*)

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ABSTRACT

Evidence of cognitive complexity in birds has led to the recognition that mammalian and avian species likely evolved comparable high-level cognitive capacities independently. One of the most significant findings that have emerged from this area of study is the identification of a key social trait that is found in species deemed to be intelligent – the presence of long-term, high-quality partnerships. Amongst birds, parrots (along with corvids) have shown relatively high levels of both cognitive and social complexity. However, relatively few parrot species have been the subject of empirical investigation. The original research presented in this thesis explores social behaviour and cognitive capacity in orange-winged Amazons (*Amazona amazonica*) and blue and gold macaws (*Ara ararauna*). Observational research findings revealed evidence of high-quality relationships in both species, and while levels of affiliative investment were similar in orange-winged Amazons (OWAs) and blue and gold macaws (BGMs), some potentially meaningful between species differences were found in courtship feeding, allopreening, and social tolerance. Experimental research findings revealed evidence of inhibitory control in both species (as measured by performance on a transparent cylinder task), though OWAs performed significantly better than BGMs on test trials. Social learning capacities were also found in OWAs through an open diffusion experiment. Both species showed poor performance in a means-end task, yielding no evidence of causal understanding. Birds also had difficulty acquiring the loose string task, which was aimed at testing cooperative problem solving. Poor performance of both OWAs and BGMs on these tasks is believed to have been primarily due to non-cognitive factors (e.g., motivation, motor difficulty of task). Affiliative investment and performance on the social learning task were found to be positively correlated in BGMs and there was some indication that individual variation in boldness may have been associated with inhibitory task performance in BGMs.

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PREFACE

The original research presented in this thesis is the product of my own work. The observational and experimental studies presented in this thesis were conducted on parrots housed at Lincolnshire Wildlife Park. All procedures performed in these studies were in accordance with the ethical standards of the University of York. These studies were approved by the university's Department of Biology Ethics committee.

Experimental data that I collected on orange-winged Amazons, which is presented in Chapter 5 (Experiments 1 and 2, Study 1), contributed to findings published in MacLean et al.'s (2014) 'The evolution of self-control' (published in *Proceedings of the National Academy of Sciences*).

The work presented in Chapter 6 has been submitted for publication, with Lauren Hogan, Megan Lambert, Anna Wilkinson, Amanda Seed, and Katie Slocombe listed as co-authors. I was the principal investigator and was involved in all data collection. I also completed all data analyses and am first author on the manuscript. Katie Slocombe, Anna Wilkinson, and Amanda Seed assisted in conception of the research design and provided suggestions for data analyses. Lauren Hogan and Megan Lambert assisted in data collection. All co-authors contributed to manuscript edits.

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AUTHOR'S DECLARATION

I declare that this thesis is a presentation of original work and I am the sole author. This work has not previously been presented for an award at this, or any other, University. All sources are acknowledged as References.

Experimental data that I collected on orange-winged Amazons (reported in Chapter 5, Study 1, Experiments 1 and 2), contributed to findings published in:

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The experimental study reported in Chapter 6 has been submitted for publication in *Animal Cognition*:

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CHAPTER 1: INTRODUCTION

Discussions concerning the origins of complex cognition have traditionally focused on the evolution of human intelligence, and by extension, primate intelligence. However, in recent years, there has been a growth in comparative cognition research leading to two important conclusions: first, that high-level mental capacities are not exclusive to primates; and second, that comparable high-level capacities are present in species who do not share close ancestry, thereby indicating the occurrence of convergence (for e.g., apes and corvids) (Byrne, Bates, & Moss, 2009; van Horik, Clayton, & Emery 2012).

Discussions of cognitive convergence have been accompanied by close examinations of the evolutionary pressures faced by species considered to be intelligent. Hypotheses concerning the evolutionary history of complex cognition, originally devised to attempt to explain the evolution of intelligence in primates, consider the social and environmental factors that may have selected for it. Comparative research allows for more widespread and systematic investigation of these hypotheses with a larger number of species, including multiple radiations leading to independent emergence of large brains and intelligent behaviour.

The original research presented in this thesis, which investigates cognition and relationship quality in two parrot species, was devised and completed with the aim of contributing to these explorations of complex cognition and its origins. The present chapter provides the theoretical background upon which this research is based, as well as an overview of the Psittaciforme order. Through these discussions, it will be illustrated that parrot research represents a valuable opportunity to broaden our understanding of various key issues, including the extent to which complex cognition is

present among avian species and the social and environmental factors that may have influenced the development of specific cognitive capacities.

Complex cognition, convergence, and the origins of intelligence: Theoretical background

Historical context. Contemplations about animal psychological processes and the degree to which they are similar to humans' can be traced back several centuries, beginning with early philosophers. While some great thinkers, like Aristotle, attributed human-like characteristics to animals (for e.g., the ability to experience emotions like jealousy and rage), others, like Descartes, viewed them as being machine-like, lacking cognition and only capable of reflexive responses (Roberts, 1998). Although these perspectives varied greatly, many shared the common belief that animals lack the ability to reason. It is a notion that was commonly taken as evidence of the uniqueness of humans, and contributed to ideas about there being a complete and inherent division between man and animal. These ideas largely went unquestioned until the publication of Darwin's theory of evolution (Roberts, 1998).

The notion of a shared ancestry among all species, including humans, had significant implications for the assumed psychological divide between humans and animals. With Darwin's observations and conclusions came the realization that behavioural and psychological continuity should exist between humans and animals (Roberts, 1998; Wasserman, 1993). Darwin expressed this idea in what has become one of his most commonly cited statements, "... differences in mind between man and the higher animals, great as it is, is certainly one of degree and not of kind" (Darwin, 1871, p.105). This continuity hypothesis, though highly controversial and rejected by

many at the time, found some initial support in anecdotal reports of seemingly intelligent behaviour by captive and wild animals. Limitations of such reports, however, were identified by researchers who argued in favour of a controlled and scientific approach to the study of animal behaviour. This task was first fully undertaken by the behaviourists, a group of early psychologists focused on the systematic investigation of behavioural processes through experimental research.

Behaviourists, such as John B. Watson, rejected the study of cognition, focusing entirely on the study of observable behaviour. This was due in part to the belief that mental processes could not be empirically measured, but primarily due to the belief that all behaviour, including seemingly complex behaviour, could be explained through simple stimulus-response associations (Hockenbury & Hockenbury, 2012). This claim, which was heavily supported by experimental research, had a significant impact on the direction of animal studies for a number of decades. Investigations aimed at understanding the nature of animal cognition were essentially abandoned until the cognitive revolution, in the 1960s (Wasserman, 1993).

As the cognitive revolution unfolded, processes such as memory and attention increasingly became topics of investigation in both human and animal research. This renewed interest in mental capacities was accompanied by the important recognition that research had been too narrowly focused on a limited number of species, mainly those considered to be the 'typical' lab animals, such as pigeons and mice (Wasserman, 1993). Interest in a wider variety of animals grew and species representing more taxa increasingly became subjects of investigation. This renewed interest in cognition was not only influential in the lab, but also in the field, leading many to consider the relationship between a species' mental capacities and its natural environment (Roberts, 1998). Highly related to this change in research direction was the emergence of

cognitive ethology, a field that aimed to understand mental adaptations within a natural context. In stark contrast to the behaviourists, cognitive ethologists considered mental states such as awareness and intention when interpreting animal behaviour (Shettleworth, 1998). While the staunch behaviourists argued that all behaviour can be explained by simple learning mechanisms, the cognitive ethologists ascribed consciousness to non-human species when analysing their interactions with their physical and/or social environment. These two opposing schools of thought represent extreme positions concerning underlying causes of animal behaviour.

Theoretical approaches to comparative cognition. Although there has been great expansion of comparative research in the last few decades, it is still largely characterized by two basic theoretical approaches: the anthropocentric and the ecological (Shettleworth, 1998). The anthropocentric approach assumes continuity between humans and animals in many general processes, such as memory, using human cognition as the model against which mental capacities in other species are measured. It therefore focuses on information processes found in humans. In contrast to the anthropocentric approach, the ecological approach is more animal-centred. It focuses on species' adaptations, considering the functions that cognitive capacities may serve within a natural context. The ecological approach thus emphasizes how cognition is used by a species in its natural habitat, applying evolutionary theories and analyses to cognitive research (Shettleworth, 1998).

These different approaches not only influence the questions researchers ask and the scientific objectives they set out to fulfil, but also the types of methods and tools they use. Naturalistic observation, for instance, is more commonly employed by researchers who approach cognition from the ecological approach, as compared to the

anthropocentric approach. It is important to stress however, that experimental research is absolutely fundamental to addressing research questions concerning cognition across all theoretical perspectives. The high degree of control and manipulation of variables allow distinctions to be made regarding the types of processes that may underlie behavioural responses. This is critical because simple explanatory factors, such as instinctual drives or basic associative learning processes, can give rise to impressive behaviours that may not involve any high-level cognitive capacities, such as causal understanding. It is thus necessary to first eliminate alternative explanations, before determining that high-level cognitive capacities offer the most plausible explanation for observed behaviour(s). Unfortunately, experimental results (and what they suggest about the cognitive capacities a species may possess) are not always clear. In many instances, results can be interpreted in more than one way, leading to conflicting conclusions. Debates concerning complex cognition, the mechanisms that drive it, the specific capacities that define it, and what makes human cognition unique, are among the most intense discussions in the field.

The debate over complex cognition: What does it mean to be intelligent?

Despite significant growth in studies aiming to understand mental processes, there is still much that remains unclear about the nature of cognitive systems involved in capacities such as problem-solving, decision-making, and causal understanding. Because these are systems of the mind, internal and therefore not directly observable, researchers are faced with the challenge of developing theoretical models that may explain capacities of interest. As Conway (2005) observes, "... in the pursuit to explain intelligence in terms of cognitive mechanisms, the best we can do is apply current

models of cognition to investigate differences, while remaining cognizant of the fact that our understanding of cognitive mechanisms themselves is limited” (p. 47).

Theoretical models of cognition tend to fall into one of two broad categories – general processes models or models of modularity. The former proposes that various behaviours/capacities are made possible by a single, general process, or system. Associative learning, for instance, has widely been identified as being a general process which is employed in various contexts, is found across species, and can give rise to an array of behaviours (Hockenbury & Hockenbury, 2012; Roberts, 1998; Shettleworth, 1998). Modular models, on the other hand, characterize cognition as being composed of various domain-specific mechanisms, described as being “self-contained and functioning independently” (Shettleworth, 2012, p. 2796). This point of disagreement is highly relevant to perspectives on intelligence as it means that consensus is lacking regarding whether it is mainly a general capacity, a mental resource that is tapped into in a variety of situations to solve various problems, or whether it is made up of separate, highly specialized capacities designed to process specific types of information.

The extent to which human cognition is unique has also been central to discussions concerning the nature of intelligence and the mechanisms that underlie it. While there is an abundance of evidence of cognitive continuity between human and non-human species, the extent of this continuity is unclear. Several authors have identified specific capacities as being points of divergence between humans and animals, such as the ability to reason about high-order relationships, while others have proposed broader theoretical models of human cognition (Shettleworth, 2012). The dual process model, for instance, theorizes that adult human cognition includes two processes that coexist, one which is evolutionarily older, basic, and is found in other

species, and another, which emerged more recently, is more complex, and is unique to humans (Shettleworth, 2012). While providing helpful theoretical starting points, it is clear that a lot more comparative research is needed in order to assess the validity of these perspectives. If we are to be able to identify aspects of human intelligence that truly are unique, then a great deal more needs to be learned about intelligence in non-human species. Among the many challenges to meeting this objective is coming to a consensus regarding how intelligence is defined and behaviourally expressed in non-human species.

The extent to which cognition is considered to be complex has been associated with several factors, including number of mental processes involved in an action, complexity of integration of mental structures, and whether abstraction is used (de Waal & Ferrari, 2010; Matlin, 2002). According to Funke (2010, p. 133), complex cognition can be understood as “active and goal-directed information processing,” which involves simple processes (e.g., perception, memory, or learning), but integrates them so as to allow for well-organized actions to be carried out by an individual. The elaborate integration of basic and complex mental structures thus makes it possible for individuals to reason, plan ahead, and solve problems (Funke, 2010; Marino et al., 2007).

Animal intelligence has traditionally been measured according to “a hierarchy of learning processes,” whereby habituation and associative learning, the most basic and widespread forms of learning, occupy the first two tiers (Shettleworth, 1998, p. 569). These processes are then followed by learning and problem solving that is more complex. This is a general process perspective, whereby differences in performance on cognitive tests tend to be seen as resulting from quantitative differences in cognition, as opposed to qualitative ones. It is an approach that Emery (2006) identifies as being

anthropocentric, noting that it fails to consider species' evolutionary histories and the cognitive adaptations they may have experienced in response to socio-ecological challenges. The general process perspective has also been criticized by those who are sceptical of conclusions based on animals' problem solving performances in laboratory settings (due to concerns regarding ecological validity) (Shettleworth, 1998).

Those who focus on the adaptability of cognition as being essential to understanding its processes, suggest that intelligence can best be understood by considering the specific types of problems animals are likely to encounter within their natural environment. It has been widely argued that, like physical traits, cognitive processes are shaped by the environmental pressures a species faces throughout its evolutionary history (Byrne & Bates, 2007; Emery, 2006; Shettleworth, 1998; van Horik et al., 2012). Researchers who approach intelligence from this perspective, have suggested that the distinction between low and high-level cognition comes down to the extent to which cognitive adaptations can be utilized in flexible ways, such as when an animal uses previous experience to solve a novel problem (Humphrey, 1976; Roth & Dicke, 2005; Seed, Emery, & Clayton, 2009). Cognitive and behavioural flexibility, have therefore been commonly identified as being hallmarks of intelligence (Emery & Clayton 2004; Humphrey, 1976; Roth & Dicke, 2005; van Horik et al., 2012). Humphrey (1976), for instance, states that intelligence is demonstrated when an animal appropriately adjusts his behaviour in response to newly acquired information. This type of act would indicate the presence of flexibility, and possibly some form of 'understanding,' – thinking about a domain, whether physical or social, in a logical manner (Emery & Clayton, 2004). Although there is still much uncertainty about how best to define intelligence, especially as it relates to non-human species, views which

focus on the flexibility of cognition provide a basic framework upon which judgements can be made about the extent to which animal cognition is complex.

The rapid expansion of comparative research that has taken place in the last thirty years or so has had a dramatic impact on contemporary perceptions of high-level cognition, and in particular, the degree to which it is unique to humans. Among reports of complex cognition which have had the greatest impact on the direction these discussions have taken, are those concerning species which are most distantly related to primates, such as dolphins and corvids. Findings which indicate similarities in the mental capacities of these animals have been particularly influential, as they have provided evidence of cognitive convergence (Connor, 2007; Emery & Clayton, 2003, 2004, 2009; Emery, 2006; Marino, 2002; Seed et al., 2009). The preceding discussion provides a couple of examples of such findings.

Convergent evolution of complex cognition. Evolutionary convergence refers to the process by which species develop similar characteristics as a consequence of having been confronted with similar evolutionary pressures, and not as a result of having inherited such traits from a shared ancestor. The case for convergence is therefore made strong when the phylogenetic separation between species is extensive (Marino, 2002; van Horik et al., 2012). Flight, for instance, is commonly cited as an example of convergence. Although distantly related, and vastly different in many respects, birds, bats, and insects share this trait in common. The wing, having evolved multiple times, but with structural differences, therefore serves as an example of functional convergence with structural divergence (Marino, 2002; Seed et al., 2009; van Horik et al., 2012). As stated in the preceding discussion, cognitive processes are subject to selective pressures just as anatomical traits are. One can therefore

reasonably conclude that cognitive similarities among species that do not share close ancestry, likely developed independently as a result of similar evolutionary forces. It is believed that through this process, capacities associated with complex cognition have emerged multiple times in various groups of animals.

Because flexibility has widely been identified as being a hallmark of intelligence, comparative researchers have paid particular attention to observational and experimental evidence of this trait (Amici, Aureli, & Call, 2008; Bird & Emery, 2009a; Bond, Kamil, & Balda, 2007; Hunt & Gray, 2003; Sargeant & Mann, 2009; Stokes & Byrne, 2001). Within the natural context, occurrences of ‘innovations’ - when animals use novel techniques to find solutions to problems they encounter- provide examples of flexibility (van Horik et al., 2012). Innovative behaviour, particularly in the context of foraging, has been reported in several species, including primates and birds (Lefebvre, Reader, & Sol, 2004). These findings have been supported by experimental studies which have measured animals’ abilities to use previously learned information flexibly; both primates and corvids have demonstrated the capacity to solve novel problems through the application of a general rule acquired during previous learning experiences (Emery & Clayton, 2004). The ability to think and act flexibly, as opposed to being relegated to automatic responses triggered by specific stimuli, has provided clear evidence that high-level cognition is not solely a primate characteristic. Additionally, evidence of a high degree of intelligence in non-primate species has come from research investigating the capacity for self-recognition, which is believed to provide the foundation for self-awareness (eg., dolphins: Marino, 2002; magpie: Prior, Schwarz, & Gunturkun, 2008).

The accumulation of evidence favouring the convergence argument has not only led to a re-examination of traditional views on intelligence and its origins, but also a re-

assessment of brain evolution and the neuroanatomical requirements for the emergence of complex cognition (Butler & Cotterill, 2006; Emery, 2006). It is an area of study which is quite vast and complex, but is a critical element of discussions concerning the evolution of intelligence. The following section provides a brief overview of some key findings relevant to this discussion.

Cognitive convergence despite neuroanatomical divergence. One of the reasons why the primate-cetacean comparison has been of such great interest is that it serves as an example of species which show significant differences in size and organization of major brain regions, while also showing clear similarities in cognitive capacities. Marino (2002) explains that while the primate brain shows a high degree of elaboration of the frontal lobes, the cetacean brain shows no such expansion. Instead, elaboration of the temporal and parietal areas characterizes the cetacean brain. This has been deemed significant due to associations found between frontal lobe expansion and evolution of intelligence in primates. Evidence suggests, for instance, that the presence of self-awareness relies on the pre-frontal cortex, which is particularly pronounced in humans and apes (Marino, 2002). The finding that dolphins possess the capacity for self-recognition was therefore particularly surprising, calling into question assumptions made about cortical requirements for the development of self-awareness.

Demonstrations of cognitive abilities which far exceed basic associative learning by birds, despite the lack of a neocortex, has also led to a re-thinking about the relationship between neuroanatomy and cognitive complexity (Emery, 2006; Zorina & Obozova, 2012). As the neocortex is the brain region most closely associated with high-level cognitive functions, such as the ability to reason and think abstractly, it has been argued that its relative size provides an adequate measure of ‘cognitive potential’

(Dunbar, 1998; Seed et al., 2009). This suggestion has been supported by the fact that humans, apes, cetaceans, and elephants top the list of relative neocortex size (as well as relative brain size), all of which demonstrate complex cognition (Connor, 2007; Roth & Dicke, 2005; van Horik et al., 2012). This measure, however, does not apply to birds, which lack the layered neocortex typical of the mammalian brain (Emery, 2006). Relative forebrain size has instead been used as a measure, due to analyses indicating a link between relative forebrain size and cognitive capacity in birds (Lefebvre, Gaxiola, Dawson, Timmermans, Rosza, & Kabai, 1998; Lefebvre, Whittle, Lascaris, & Finkelstein, 1997; Nicolakakis & Lefebvre, 2000). Findings of cognitive convergence, despite divergence in some key neuroanatomical features, have led to close examinations of the selective pressures faced by 'intelligent' species. This task has been undertaken by many researchers seeking to identify explanatory factors associated with cognition, in the hopes of addressing fundamental questions regarding the evolution of intelligence (Byrne & Bates, 2007; Marino, 2002; Seed, et al., 2009; van Horik et al., 2012).

Questions raised by evidence of cognitive convergence. Similarities in complex cognitive capacities among primate, cetacean, and avian species (among others) raise two basic, but crucial questions: *why* and *how*? Although there is little debate regarding the notion that intelligence, in a general sense, is functional and therefore adaptive, it is not necessary for survival. After all, plenty of species have survived and thrived despite the apparent lack of such capacities. Additionally, it has been pointed out that possessing a high degree of intelligence is “in many ways a costly and inefficient way of acting in the world” (Seed et al., 2009, pg. 402); this is because of the investment of time and energy that is required to develop complex cognition.

Unlike innate or simple associative learning processes, which allow animals to respond to their environment immediately (or soon) after birth, high-level cognition requires a developmental period during which an individual acquires information about their environment and learns how to use it in an effective way (Seed et al., 2009).

Why, then, has complex cognition evolved in these various species? This question brings us back to the issue of flexibility. It has been suggested that instinctual or conditioned responses may be too rigid to effectively deal with environmental factors that do not remain consistent (Emery & Clayton, 2004; Humphrey, 1976). Flexibility in cognition would, for instance, allow an individual to apply previously acquired information to solve a problem never before encountered. This, however, raises further questions, including: What are the environmental factors that require this level of flexibility? And, how have they shaped the cognitive processes found in these 'smart' species?

Shared traits: Explaining why and how complex cognition evolved.

Investigations of factors that may have been fundamental to the emergence of advanced mental processes have identified several biological, behavioural, and ecological similarities among cognitively complex species. These include the following: large relative brain size, long developmental periods and life histories, flexible and innovative behaviour, living and foraging in unpredictable environments, and the presence of complex social organization and behaviour (Connor, 2007; Marino, 2002; Seed et al., 2009; van Horik et al., 2012). These are traits which have been deemed necessary for the emergence of intelligence and have provided the basis for numerous hypotheses about its origins (Shettleworth, 1998; van Horik et al., 2012). At the centre of many of these theories are comparative analyses of brain size.

Despite structural differences, the brains of intelligent animals, such as apes, dolphins, and corvids, have an important trait in common –they are significantly larger than that expected for their body mass; larger than is necessary for survival (Dunbar & Shultz, 2007; van Horik et al., 2012). Expansion of the brain and the relative size of a species' brain (or components of the brain) have been seen as key to understanding the emergence of intelligence (Connor, 2007; Dunbar, 1998; Emery, 2006; Lefebvre et al., 2004; Shultz & Dunbar, 2010). Because it is physiologically costly to maintain such a large and complex organ, it stands to reason that this increase in size and neural complexity must have allowed for advancements in cognitive processes. This conclusion has influenced investigations aimed at identifying traits and factors that are associated with, or necessitated, the expansion of the brain. Brain size measures are therefore commonly cited as providing evidence in support of intelligence origins hypotheses, essentially used as an anatomical proxy for intelligence (MacLean et al., 2012).

In their discussion of cognitive and behavioural convergence in corvids and apes, Seed and colleagues (2009) summarize several hypotheses aimed at explaining the evolution of primate intelligence. They consider evidence for and against each hypothesis, as well as the extent to which they can be applied to corvids or other species. These potential explanations are organized into two broad categories: those which concern the physical environment and those which concern the social environment. In the physical domain, food access and distribution is the primary focus. It has been argued that greater memory capacity and behavioural flexibility is required in omnivorous species that rely on foods which occur in patchy and unpredictable distributions (varying across time), and/or require extractive foraging. It is suggested, for instance, that these foraging conditions may have selected for the development of

cognitive maps and/or innovative foraging strategies, such as tool use (Byrne & Whiten, 1997; Seed et al., 2009). Initial support for these ideas came from analyses of relative brain size in primates, which found it to be correlated with these three factors (omnivorous diet, unpredictable foraging environments, and extractive foraging). However, when further analyses were conducted, using neocortex size as the brain size measure, no such relationship was found (Dunbar, 1998). Furthermore, various avian brain size analyses did not find size to be associated with diet in birds (Shultz & Dunbar, 2010). Indicators of social complexity, however, have been found to be highly correlated with relative brain and neocortex size in mammals, as well as relative brain size in birds (Dunbar, 1998; Shultz & Dunbar, 2010).

Associations between brain size and sociality, in conjunction with the observation that behavioural complexity appears to be most pronounced within the social domain, have led to speculations about how group life contributed to the emergence of higher cognition (Dunbar & Shultz, 2007). It has been argued that life in a group has both allowed and selected for the development of behavioural and cognitive flexibility. Connor (2007) explains that while sociality provides several benefits, such as being able to cooperate in securing resources, fending off potential attackers/competitors, and rearing offspring, it also has its costs, putting group members in close competition with one another for valuable resources. He further explains that the benefits allow for long developmental periods and long life history, which make it possible to accumulate knowledge from others and one's own experiences; however, it means that animals are simultaneously competing with, and are dependent upon, the same individuals (Connor, 2007). It has thus been argued that the challenges presented by social life selected for mental adaptations which allow individuals to manage their interactions with others in a flexible and effective manner

(Humphrey, 1976; Byrne & Whiten, 1997; Emery, Seed, von Bayern, & Clayton, 2007).

Sociality as a key factor in the emergence of complex cognition. The notion that sociality has been instrumental to the evolution of human and animal intelligence is rooted in early observational research. Jolly (1966) was among the first to suggest that primate group life likely preceded the development of intelligence. It was a conclusion that was based on field studies of lemurs. Jolly found that while lemurs did not demonstrate the level of cognitive complexity found in monkeys, they were nonetheless highly social. It was thus concluded that group life must have developed prior to the emergence of high-level cognition. This perspective was expanded upon by Humphrey (1976) in his seminal paper, “The Social Function of Intelligence,” in which he argues that primate intelligence evolved due to the adaptive pressures imposed by complex social life. This idea, referred to as the ‘Social Intellect Hypothesis’ (SIH), is based upon the observation that sociality introduces certain social-ecological challenges that are not experienced by creatures leading solitary lives.

As previously indicated, although sociality provides certain benefits, such as added protection from predators and being able to cooperate in securing resources, it does not necessarily mean an easier life. A social animal is not limited to concerns involving food, predators, and procreation. It must also contend with the unpredictable nature of life with conspecifics and find its place within the social structure that makes up its group. These added factors make life more challenging, and as a result, an inherent value is found in the ability to successfully compete with fellow group members by effectively managing social dynamics (Humphrey, 1976). Byrne and Whiten (1988) considered these social pressures and put forth the ‘The Machiavellian

Hypothesis,' arguing that intelligence has its roots in social manipulation, including deception and strategic cooperation. As these ideas were further investigated, supporting evidence (from the field and the lab) began to accumulate. One of the more significant findings relates to brain size. In Dunbar's (1998) original analysis of the relationship between sociality and brain size, it was found that primate social group size, used as a measure of social complexity, was significantly related to neocortex size. 'The Social Brain Hypothesis' (SBH) thus emerged, linking the expansion of the neocortex, which is responsible for executive functions, to the ability manage information acquired within the social domain, particularly about relationships (Dunbar, 1998).

Re-thinking social intelligence hypotheses. Although these hypotheses were originally aimed at explaining primate, and ultimately human, intelligence, they have more recently been applied to other animals as well. This has been due to the recognition that complex cognition is also found in non-primate species (Emery & Clayton, 2004; Marino, 2002). The relationship between group size and brain size, for example, has also been identified in four other mammalian taxa, including toothed cetaceans (Dunbar, 1998). Like apes, dolphins live in socially complex environments that are comprised of multiple relationships and often change in size and organization. It has therefore been argued that it is the need to learn about several social relationships, and to use this information to successfully compete for resources, that led to complex cognition and flexible behaviour. This proposition, however, has been re-examined and contested as a result of avian research (Emery, Clayton, & Frith, 2007).

The abundance of strong evidence pointing to the presence of complex cognition in several avian species, particularly corvid species, has caused some

researchers to question the supposed importance of group size in the emergence of intelligence (Dunbar & Shultz, 2007; Emery, Seed, et al., 2007). This is because such a relationship is not found among birds (Dunbar & Shultz, 2007). Emery and colleagues explain that avian social systems are highly variable, both within and across species, often changing depending on where they live and what time of year it is (Emery, Seed, et al., 2007). Because avian group size fluctuates, they argue that another measure of social complexity should be used when considering the relationship between sociality and cognition. The authors therefore propose a revision to SIH and SBH, one which redefines ‘social complexity’ and identifies a key similarity found in the social interactions typical of corvids, parrots, apes, and dolphins – bonding and long-term partnerships.

Emery and colleagues observe that initial discussions examining the relationship between group size and potential intelligence, as indicated by neocortex size, emphasized quantity as the defining feature of ‘social complexity’ (Emery, Seed, et al., 2007). They, however, argue that what matters most in social relationships is not the number of individuals one interacts with, but the *quality* of those interactions. Because the mated pair is the most stable structural component of most avian societies, the authors explore the role ‘life-long monogamy’ may have played in the expansion of the avian brain, resulting in greater cognitive abilities. They argue that large-brained bird species who maintain life-long pair bonds are characterized by a form of ‘relationship intelligence,’ which allows them to become ‘in tune’ with their mates. It is further suggested that this provides them with a competitive advantage over individuals that lack such partnerships.

To further investigate the idea that the quality of the pair bond is a significant factor in this relationship, Emery and colleagues compared the brain sizes of distantly

related avian species that engage in life-long monogamy. This analysis included species belonging to four avian groups: anseriformes (e.g., ducks and geese), corvidae (e.g., crows and rooks), psittaciformes (parrots and conures), and procellariiformes (e.g., albatrosses and petrels) (Emery, Seed, et al., 1997). The brains of corvids and parrots were found to be the largest, with the differences being highly significant. The authors present this finding as providing support for 'The Relationship Intelligence Hypothesis' (RIH), arguing that the relationship between mates is more complex, both socially and cognitively, in corvids and parrots as compared to geese and albatrosses (Emery, Seed, et al., 2007). The difference in complexity can be seen in the extent to which partnerships are actively maintained throughout the year. The authors explain that while geese and albatrosses pair up with the same individuals each breeding season, from year to year, they do not maintain close proximity nor engage in affiliative behaviours (such as allopreening or providing support during agonistic encounters) outside the breeding season. Corvids and parrots, however, do, investing time and energy to maintain and strengthen the bond.

Discussions examining differences between large-brained and small-brained birds have prompted more comprehensive analyses. Initial investigations discovered a strong association between brain size and several life-history traits, with large brained birds being born highly immature and vulnerable (altricial development, as opposed to precocial), experiencing long developmental periods, and high parental investment (Shultz & Dunbar, 2010). A more comprehensive investigation was conducted by Shultz and Dunbar, in which they compared 135 bird species on a wide variety of factors. The aim of their study was to identify which traits are most closely associated with brain size (measured in various ways), as well as to examine phylogeny in relation to brain size expansion. They looked at such things as developmental state at hatching,

diet, migratory status, pair bond duration, and foraging group structure. The results revealed that brain size was associated with pair bond duration, stable social groups and bi-parental care, with the strongest correlation being with pair bond duration. Furthermore, 'evolutionary contingency' analyses indicated a significant shift in parental investment, representing an adaptive change that was crucial to brain expansion. Shultz and Dunbar conclude that the establishment of bi-parental care, in which both the male and female cooperate in the rearing of their young, led to pair bond formation. It is further suggested that these partnerships made altriciality and the development of large brains possible. Based on these findings the authors speculate about the relationship between pair bonding and cognition; they suggest that the coordination and cooperation required in order to successfully rear altricial young imposes significant cognitive demands. Shultz and Dunbar conclude by acknowledging that the findings lend support to RIH, affirming Emery et al.'s (2007) claim that relationship quality is more important than the number of conspecifics one interacts with.

In Dunbar's (1998) initial assessment of the relationship between brain size and social complexity, he acknowledges that group size is only one feature of social complexity, serving as a 'simple measure.' Due to the limited scope of initial investigations, further studies were conducted. Analyses of brain evolution and size in birds and mammals found a highly significant relationship between relative brain size and the evolution of sociality; additionally, a relationship between large relative brain size and pair bonded monogamy was found in all taxa, with the exception of anthropoid primates (Dunbar & Shultz, 2007). It should be noted that cetaceans were not part of this analysis. The authors suggest that although pair bond monogamy is not part of the social organization of anthropoid primates, strong bonds are. Apes, like dolphins, form

and maintain long-term partnerships that function much like pair bonds. Although these alliances are not formed for reproductive purposes, their adaptive value and social complexity are akin to that which is found in corvid pair bonds (van Horik et al., 2012).

Based on observations of social interactions involving pair bonds/alliances, it can be concluded that they require the ability to competently read social signals and adjust behaviour on the basis of those signals. This conclusion is supported by Shultz & Dunbar (2010) in their revision of the social brain hypothesis. The authors consider the results of their findings, that pair bonding strongly correlates with relative brain size in birds and several mammalian groups, and suggest that what appears to be of greatest significance in the evolution of the 'social brain' is the need to negotiate and coordinate with others. Furthermore, because these partnerships exist and function within a larger social environment, one which puts individuals in competition with each other over resources, there is also a need to learn about other alliances/pair bonds. As a result, the ability to pay attention to, and learn about, individual characteristics and third party relationships is of great value. The pressures associated with this type of social relationship, it is believed, select for cognition that is flexible and complex (Byrne & Bates, 2007; Byrne & Whiten, 1997; Connor, 2007; Dunbar, 1998).

As the previous discussion clearly illustrates, there has been a tremendous reliance on brain size measures in the quest to understand the selective forces that have influenced the development of complex cognition. It is important to note however, that although this practice (correlating brain size with ecological variables) is widespread, it does not mean that it is without its flaws. If scientists are to develop an accurate understanding of the nature of the relationships that exist among brain size, ecological factors, and complex cognition and behaviour, then it is necessary to acknowledge these methodological issues and work towards addressing them.

Limitations of brain size analyses. In their discussion of the use of brain size analyses as a means of investigating complex cognition and the factors that are linked to it, Healy and Rowe (2007) identify several major limitations that should be considered. The first deals with the ways in which brain size is defined functionally. The authors explain that brain areas which are associated with complex cognitive processes are involved in the production of several behaviours. This makes it problematic to draw conclusions about the role that a specific trait may have played in the expansion of a certain brain region. The authors additionally note that there are significant variations in the types of procedures researcher use to measure brain size; these inconsistencies, they point out, can lead to inaccurate and misleading results. Healy and Rowe also focus much of their discussion on the wide variety of variables that have been correlated with brain size. They suggest that there are significant challenges to operationally defining traits such as behavioural flexibility, which also imposes limitations on the conclusions that can be made. They additionally argue that there has been little consideration for how variations in development and experience may impact brain size analyses. It is explained that data sets are likely to include brain size measures from individuals in various stages of development and with various levels of experience (such as experiencing different degrees or types of environmental stimulation), each of which are known to impact brain size. Finally, the authors urge research to move towards integrating the various hypotheses that have emerged from comparative brain analyses in a meaningful way. They suggest that an attempt should be made to develop a comprehensive theoretical framework that can account for the various relationships found in brain size research. It is a task which will require the use of experimental research, along with phylogenetic analyses; this will allow investigators

to determine when specific cognitive and neuroanatomical changes took place in a species' evolutionary history.

Where do we go from here? Comparative research has had a dramatic effect on the way we understand cognition, including its mechanisms, variations, and origins. The cognitive and behavioural similarities found among distantly related species has thus far provided compelling evidence of cognitive convergence. In addition, extensive analyses of species specific traits, including ecological, social, and neurological factors, have provided insights into the adaptive pressures that may have given rise to capacities associated with intelligence. These achievements, though highly significant, are just the beginning of a long scientific journey that will require large-scale collaboration among researchers, as well as the application of various research tools and methodologies.

The need for more widespread and systematic research has been addressed by several authors. MacLean and colleagues (2012, 2014), for instance, emphasize the importance of integrating comparative psychology and evolutionary biology. They demonstrated that quantitative procedures that have been developed to investigate the phylogenetic distribution of traits can be used in conjunction with comparative experimental research. MacLean and colleagues (2014)¹ tested 36 species on the same problem solving tasks. They investigated the extent to which various socio-ecological and neuroanatomical factors could explain the variance that was observed in cognitive performance across species; absolute brain size was found to be the strongest predictor of inhibitory control. MacLean and colleagues argued that large-scale comparative

¹ Data presented in Chapter 5 (Study 1) contributed to MacLean et al.'s (2014) findings

investigations such as the one they conducted make it possible to determine how predictive phylogeny is of cognitive variation, as well as to identify the point at which major cognitive changes took place throughout evolutionary history (and what prompted them).

Parrots: an untapped resource. Now that the foundation has been laid for the development of a broader and more accurate comprehension of the evolution of intelligence, there must be greater focus on studying species that have undergone little (or no) cognitive investigation. The discovery of complex cognition in corvid species, as previously discussed, has provided some of the most persuasive evidence of the occurrence of cognitive convergence. However, the extent to which this is unique among birds remains unclear.

Several suggestions have been made that in addition to corvids, parrots possess high-level cognition. Although this assertion is based on some empirical evidence, it has not been adequately supported due to the general scarcity of parrot cognition research. However, what is known about them seems to suggest that complex cognitive processes may be present throughout this avian order.

Psittaciformes

Parrots, commonly referred to as psittacines, consist of approximately 350 bird species that make up the order Psittaciformes (Forshaw, 2006). They are currently classified as being one of two orders that make up the Psittacopasserae taxon (the other being the Passeriformes), and are identified as being comprised of three superfamilies, including the *psittacoidea* (referred to as the ‘true parrots’), the *cacatuoidea* (made up of cockatoo species), and the *stigapoidea* (made up of a small group of New Zealand

parrots) (Joseph, Toon, Schirtzinger, Wright, & Schodde, 2012). Although highly varied in size and coloration, parrots are among the most recognizable of all avian groups. Several morphological features, such as mandible size and shape (short and rounded with a downward curve), toe composition (two pointing forward and two pointing backwards) and the presence of a thick prehensile tongue, characterize psittacines and make them distinguishable from other avian orders. The vast majority of parrot species live in tropical and subtropical regions, with wild populations residing in South America, South East Asia, West Africa, India, and Australia (Forshaw, 2006; Waterhouse, 2006). Although wild parrots can be extremely difficult to study due to their arboreal lifestyle and large home ranges, several studies have successfully documented natural parrot behaviour (Beissinger, 2008; Brightsmith & Bravo, 2006; Pitter & Christiansen, 1997; Renton, 2004; Renton & Salinas-Melgoza, 1999). What is presently known is summarized in the following section. It is important to note, however, that while the characteristics described below are representative of most psittacines, they are not necessarily representative of all species.

Parrot Phylogeny. In the last couple of decades, there has been a significant increase in research aimed at understanding parrot evolution. This has been part of a larger interest in bird phylogeny, and has been influenced by significant developments in biological research methods, such as the development of DNA sequencing (Schweizer, Seehausen, & Hertwig, 2011). Although debates persist regarding which specific fossils represent the earliest parrot specimens, there is general agreement that the ancestors of modern parrots were in existence by the end of the Cretaceous period, having originated in the prehistoric supercontinent known as Gondwana (Schweizer et al., 2011; Waterhouse, 2006). The Psittaciforme split from the stem lineage is

presently believed to have taken place approximately 58 million years ago (mya) (Schweizer et al., 2011), with psittacine species being widespread and diversified by the Early to Middle Miocene period (23-11 mya) (Forshaw, 2006).

Due to fossil discoveries and advancements in phylogenetics, the Psittaciforme order has undergone several changes in classification (Joseph et al., 2012). Until recently, the order was described as being made up of two superfamilies, *psittacoidea* and *cacatuoidea*. However, comprehensive research, consisting of morphological and genetic analyses, has led to the re-classification of New Zealand parrots. They are now classified as making up a separate superfamily, the *strigapoidea*, having been removed from the *psittacoidea* superfamily (Joseph et al., 2012). The following discussion includes an overview of the three superfamilies that make up the Psittaciforme order, as well as a summary of traits parrots share with corvids that are indicative of cognitive complexity.

Psittaciform superfamilies.

***Psittacoidea*:** The *psittacoidea* are the largest of the Psittaciforme superfamilies, known as the ‘true parrots.’ The vast majority of extant parrot species belong to this superfamily. Most are found in tropical climates, living in woodlands or rainforests (Forshaw, 2006). Among the *psittacoidea*, are species occupying regions of South America, such as the macaws and Amazons. They are among the most recognizable of all the psittacines. Consisting of six living species, macaws include some of the largest parrot species. The hyacinth macaw (*Andorhynchus hyacinthinus*), for instance, measures up to 100 cm in length and weighs between 1200 and 1450g (Forshaw, 2006). Less well known is the smallest macaw, the Red-shouldered macaw (*Diopsittaca nobilis*), measuring just 30cm in length, and weighing approximately 130g (Forshaw,

2006). Considered by many to be extremely beautiful, several macaw species have become highly valued in the pet trade. Amazons, which are medium-sized parrots that are largely green in colouration, are also quite popular in the pet trade. Though generally not considered as physically striking as the macaws, Amazon parrots have garnered attention for their ability to engage in vocal mimicry (Hoppe, 1992). It is an ability that is not unique to Amazons, but is also found in other species, such as African greys (*Psittacus erithacus*), which are widely recognized for their impressive ability to mimic human speech patterns (Pepperberg, 1994, 2006). The African greys are a native species of west and central Africa, found mainly in lowland forest (Forshaw, 2006). They are perhaps the most extensively studied parrot species (in terms of cognitive research), and have been found to perform impressively on some cognitive tests (to be reviewed in Chapter 2).

While the previous examples of *psittacoidea* species described represent species that are prototypical of the superfamily in many respects, eclectus parrots (*Eclectus roratus*), serve as an example of a somewhat atypical *psittacoidea* species. They can be found in New Guinea, the Solomon Islands, Indonesia, and Australia. Like most other ‘true parrots,’ eclectus show a preference for wooded habitats, are cavity nesters, and largely feed on fruits, seeds, and nuts. They, however, demonstrate extreme sexual dimorphism, which is unique among the psittacines; the males display bright green plumage, while the females display bright red and purple (or blue) plumage (Heinsohn & Legge, 2003). Additionally, they are cooperative breeders, with females mating with multiple males, who then are responsible for feeding the female and young while they are in the nest cavities (Heinsohn & Legge, 2003). This is a trait which is highly unusual among psittacines, though not unique to eclectus. Vasa parrots (*Coracopsis vasa*), which are found in wooded habitats in Madagascar, also demonstrate a

polyandrous mating system. They too show some sexual dimorphism, with females being larger than males; females also shed head feathers prior to the breeding season, revealing striking bald yellow heads (Ekstrom, Burke, Randrianaina, & Birkhead, 2007; Foreshaw, 2006).

***Cacatuoidea*:** The *cacatuoidea* superfamily is much smaller than the *psittacoidea*, comprised of approximately 21 cockatoo species (Murphy, Legge, & Heinsohn, 2003). In habitat, behaviour, and socio-ecology, the cockatoos are highly similar to most of the species belonging to the *psittacoidea* superfamily. Like the *eclectus*, cockatoos can be found throughout Australasia (Forshaw, 2006). Most are medium to large-sized and are not as brightly coloured as the ‘true parrots’ tend to be. Cockatoo plumage is generally white, grey, black, or pink. Many do, however, have impressive head crests, which make them very recognizable. The largest brains found among psittacines, belong to cockatoo species (Iwaniuk, Dean, & Nelson, 2004).

***Strigapoidea*:** The *strigapoidea* make up the smallest of the Psittaciforme superfamilies, only including two extant species that are native to New Zealand; these are the kea (*Nestor notabilis*) and the highly endangered kakas (*Nestor meridionalis*). The kea are known as mountain parrots, found living in steep-sided wooded valleys and alpine scrublands (Forshaw, 2006). Like cockatoos, keas are known for being curious and skilled problem-solvers (Huber & Gajdon, 2006). The kaka are forest dwellers, less likely to be seen in populated areas and less bold than the kea. Unlike most parrot species, keas and kakas have been found to be polygamous, with males having more than one breeding partner (del Hoyo, Elliott, & Sargatal, 1992; Joseph et al., 2012).

Behaviour and socio-ecology. In addition to foraging, which largely consists of locating edible fruits and seeds (though some species are omnivorous and also eat

insects, grubs, etc.), parrots appear to spend much of their time engaging in social interactions with conspecifics (Forshaw, 2006). Often described as highly gregarious and noisy, psittacines are regularly seen roosting in large flocks, producing loud vocalizations that tend to peak in frequency and volume during morning and evening roosts. Although there are some variations in behaviour, large flocks tend to break up into smaller foraging parties at sunrise, travelling to various feeding sites throughout the day, and coming back together late in the afternoon or early evening (Forshaw, 2006, Hoppe, 1992; Martin, 2001). It is believed that such flock formations, which may consist of hundreds of individuals, allow for greater protection of resources, and serve as a predatorial defence strategy. Although large flocks are key features of parrot social life, it has been argued that it is the reproductive pair that serves as the basis of parrot social organization (Seibert, 2006).

As previously indicated, the study of wild parrots presents some unique challenges. Among them are difficulties associated with tracking individual birds; parrots have been found to use their strong beaks to remove tracking devices. This poses a significant problem for a wide variety of studies, including those which aim to document social behaviour; as such, data on psittacine social systems is far from complete (Foreshaw, 2006; Spoon, 2006). However, based on the data that is presently available, it appears that the majority of psittacines are socially monogamous, maintaining life-long bonds with their reproductive partners (Heinsohn & Legge, 2003). This trait has been associated with the general lack of sexual dimorphism found among parrots (Heinsohn & Legge, 2003). During breeding season, reproductive pairs take ownership of cavities (cavities in trees or dug into the ground or the side of cliffs), often returning to previously used sites to lay eggs and rear their young. There are some species, however, that are an exception to this and build nests in trees (e.g.,

Quaker parrot, Harrison, 1973; rosy-faced love bird, Ndithia, Perrin, & Waltert, 2007). Some variation has been found in the degree to which males are involved in egg incubation, but bi-parental care of the young seems to be highly characteristic of parrot breeding behaviour across species (Brightsmith & Bravo, 2006; Forshaw, 2006; Heinsohn & Legge, 2003; Seibert, 2006; Spoon, 2006).

One of the most noteworthy features of parrot social monogamy is the fact that these partnerships are maintained outside the breeding season (Seibert, 2006; Spoon, 2006). This characteristic sets them apart from many other socially monogamous birds, such as geese, and is one of the reasons why parrots are commonly regarded as being socially complex (Emery, Seed, et al., 2007). Bonded pairs tend to maintain close spatial proximity, carrying out their daily activities together. They also engage in affiliative behaviours, such as allopreening and allofeeding, which are believed to play key roles in the establishment and maintenance of bonds. These affiliative behaviours, it has been suggested, may also function as social cues, revealing important information to conspecifics about partnership status (Seibert, 2006; Spoon, 2006).

The parrot-corvid comparison: Indicators of intelligence. Corvids make up the corvidae family, commonly referred to as the crow family. They are among the largest of the passerines and consist of approximately 120 bird species, including crows, ravens, jays, magpies, and nutcrackers (Brinkley, 2007; Clayton & Emery, 2007; Perrins, 2003). They are a diverse group of birds, widely known for their adaptability and intelligence. They can be found throughout the world, living in a range of habitats (Brinkley, 2007; Ericson, Jansén, Johansson, & Ekman, 2005; Perrins, 2003). Corvids are omnivores, with many eating a wide variety of plant and animal foods (Brinkley, 2007; Perrins, 2003). Many species are also known to cache food,

with several species demonstrating impressive recall capacity for the location of cached food (Brinkley, 2007; Perrins, 2003). They are considered to be clever scavengers, known to exploit various food sources, including artificial ones (Brinkley, 2007; Perrins, 2003; Hadjisterkotis, 2003).

Corvid sociality is reportedly diverse, with social organization varying within and between species, depending on a variety of environmental factors, such as seasonal changes (Clayton & Emery, 2007). However, like psittacines, the majority of corvids are monogamous, developing long-term bonds with their reproductive partners. Also like the psittacines, partnerships are maintained outside the breeding season and are characterized by frequent affiliative behaviours. Cooperative breeding, however, is more common among corvids than parrots (Perrins, 2003; Brinkley, 2007).

In addition to the formation of strong bonds, parrots and corvids share other important traits. Both encounter similar foraging challenges; they tend to rely on food items that vary temporally and spatially, and in many cases, require extractive foraging (Emery, 2006; Forshaw, 2006; Hunt & Gray, 2004). Additionally, parrots and corvids are born in an altricial state, undergoing long developmental periods that depend on bi-parental care. They have long life histories, with some parrots living up to 70 years and some corvids living up to 20 years (Brouwer, Jones, King, & Schifter, 2000). Among birds, parrots and corvids have the largest relative brain sizes and have been identified as having the highest degree of brain morphophysiological complexity (Zorina & Obozova, 2011). Zorina and Obozova describe them as being phylogenetically young due to the expansion and development of certain brain regions. They state that both parrots and corvids have “high forebrain/brainstem ratios and pronounced development of phylogenetically new neopallial structures” (Zorina & Obozova, 2011, p. 5).

As has been illustrated, parrots, like corvids, demonstrate a range of characteristics that have been associated with complex cognition. While these key similarities point to the potential for intelligence, the true extent to which parrots are cognitively complex can only be fully understood through comprehensive empirical research. Thus far, the limited research that has been conducted is promising, providing evidence of capacities such as concept acquisition, tool use, cooperative problem solving, and language comprehension (Auersperg, Szabo, von Bayern, Kacelnik, & 2012; Pepperberg, 2006; Péron, Rat-Fischer, Lalot, Nagle & Bovet, 2011). Unfortunately, these studies are limited; only a few species have been the focus of scientific investigation and most of the studies have involved very few subjects. Peron et al.'s (2011) study on cooperative problem-solving, for instance, included only three African grey parrots, while Auersperg et al.'s (2012) study on tool use, only involved one cockatoo. The generalizability of findings reported in these studies is therefore minimal, leaving many questions still unanswered about the true scope of parrot cognition and the factors it is associated with (for a summary of the studies identified, see Chapter 2).

The potential contribution of parrot research. In their review of convergent evolution of cognition in animals, van Horik and colleagues (2012) deem primates and corvids as belonging to the 'clever club,' and consider other animals that may be worthy of membership. Among those they consider are parrots. They are among several authors who indicate that parrots may serve as an additional example of convergence of complex cognition (Byrne & Bates, 2007; Emery, Seed, et al., 2007; Schuck-Paim, Alonso, & Ottoni, 2008). Although this assertion has been supported by evidence of high-level cognition in a handful of species, it is important to remember

that there are over 350 species of parrot. The tendency to describe parrots, as a group, as being cognitively superior to other birds (with the exception of corvids), may therefore be premature. Exploration of the cognitive capacities of parrot species that have yet to undergo significant study is therefore essential. It would not only provide a more accurate understanding of psittacine cognition in general, but would also contribute to our understanding of the phylogeny of avian cognition, including the occurrence of convergence.

This thesis aims to accomplish two major objectives. The first is to contribute to our understanding of parrot cognition by presenting cognitive research conducted on two South American species, orange-winged Amazons (*Amazona amazonica*) and blue and gold macaws (*Ara ararauna*). The second is to further investigate a theory that has emerged from corvid research, concerning a social factor believed to have played a role in the emergence of complex cognition – high quality long-term partnerships.

CHAPTER 2: AVIAN PROBLEM-SOLVING CAPACITIES

As indicated in Chapter 1, measures of animal intelligence commonly identify flexibility as a defining feature of complex cognition. Evidence of this trait has been identified across a range of taxa (including birds), providing support for the occurrence of cognitive convergence, and highlighting the adaptive value of cognitive and behavioural flexibility in dynamic or unpredictable environments. It has been commonly argued, for instance, that the capacity to use information flexibly allows an individual to solve a broader range of physical or social problems more efficiently than would be possible with a total reliance on reflexive responses or trial and error learning (Emery & Clayton 2004; Humphrey, 1976; Roth & Dicke, 2005; van Horik, Clayton, & Emery, 2012).

The present chapter provides an overview of avian research that focuses on capacities that are involved in, or are relevant to, flexible problem solving in the physical and/or social domains; experimental investigations of object permanence, inhibitory control, concept formation, causal understanding, social learning, and cooperative problem solving, are discussed. First, however, some historical context will be provided, as this is important to understanding the current state of avian cognition research.

Avian cognition research in historical context

The realization that high-level cognitive capacities are not restricted to mammals, but are also found among avian species, resulted from several decades of comparative research. As discussed in Chapter 1, commonly held beliefs about cognitive continuity between humans and animals and the degree to which behaviours

can be explained by simple or complex processes, have widely varied, evolving over time. These trends are heavily reflected in the literature reporting avian research, having influenced the species and types of capacities studied, and ultimately the conclusions drawn about similarities and differences between avian and mammalian cognition.

With the acceptance of Darwin's theory of evolution came a growing interest in non-human primate research, which was largely aimed at developing a better understanding of the evolutionary origins of human behaviour and cognition (Emery, 2006). The widespread focus on primate species reflected an anthropocentric approach to comparative research that also influenced commonly held beliefs about avian cognition; the recognized significance of shared ancestry shaped expectations about how similar cognitive processes would likely be among different species. Due to the significant phylogenetic separation between primates and birds, as well as the dramatic differences between primate and avian brains, the prevailing assumption throughout much of the twentieth century was that birds lacked complex cognition (Emery, 2006; Zorina & Obozova, 2012).

The perception of birds as being absent of high-level mental processes was strengthened by research that sought to identify common and fundamental behavioural and cognitive processes shared across species (Emery, 2006; McLean et al., 2012). The expansion of this experimental research focused heavily on species that were relatively easy to obtain, house, and test under laboratory conditions. Studies on birds such as pigeons, quail, and chickens therefore made up the majority of early experimental avian research. It is argued that the pervasive use of a limited number of small-brained avian species propagated ideas about the cognitive divide between birds and mammals, as it resulted in inaccurate generalizations about cognitive potential across avian taxa

(Emery, 2006). These generalizations, however, came under scrutiny as more species were investigated.

Although many studies over the last half century have contributed to the transformation of perceptions of avian cognition, corvid and psittacine research has been particularly influential in driving this change. Experimental studies have provided evidence of high-level cognitive capacities in these birds (e.g., abstract concept acquisition, Pepperberg, 1987; insightful problem solving using, Bird & Emery, 2009a,b; imitation, Moore, 1992). This evidence, in conjunction with field research reported by ornithologists and cognitive ethologists, has built a strong case against the traditional view of avian behaviour as being entirely motivated by instinct and/or associative learning (Emery, 2006; Zorina & Obozova, 2012). Substantial developments in avian brain research have also contributed to changing perceptions of avian cognition; as indicated in Chapter 1, discoveries of avian brain structures that are functionally similar to regions of the mammalian neocortex have furthered our understanding of the mechanisms that allow for primate-like intelligence in the absence of primate neuroanatomy (Zorina & Obozova, 2012).

Solving problems in the physical realm

The ability to flexibly solve problems may involve a variety of cognitive skills and executive functions, such as causal understanding and working memory. In many cases, the types of cognitive processes that individuals rely on to solve problems in the physical environment are also implicated in problem solving in the social domain. Indeed, when it comes to socially complex species, there is much debate concerning whether cognitive adaptations are responses to challenges animals encounter in their physical environment (e.g., extractive foraging), their social environment (e.g., needing

to cooperate with a partner to protect or acquire resources), or both (Byrne & Bates, 2007; Dunbar & Shultz, 2007; Milton, 1981; Seed, Emery, & Clayton, 2009; van Horik et al., 2012). The following discussion provides an overview of avian performance on physical tasks, focusing on whether birds can retain memories of objects, control reflexive responses, form concepts, or understand causal forces.

Object permanence. Defined as the ability to recognize that objects continue to exist when they are no longer being perceived, object permanence is considered to be a basic component of physical cognition (Hoffmann, Rüttler, & Nieder, 2011). This capacity relies on working memory, which is one of the major components of a set of mental capacities implicated in the control and coordination of information, known as executive functions (Willoughby, Kupersmidt & Voegler-Lee, 2012). Object permanence has been tied to reasoning ability, allowing individuals to understand the permanence of the external world and hold mental representations of it (Rathus, 2010). It is therefore seen as a critical aspect of object concept formation, which requires the recognition that objects have enduring physical properties (Johnson, Amso, & Slemmer, 2003).

Initial investigations of object permanence, which were conducted on human infants by developmental psychologist Jean Piaget (1952), revealed that this capacity is not present at birth, but instead develops in successive stages early in life. Piaget identified six stages, with the first consisting of the ability to track moving objects, and the last characterized by a complete understanding of displacement (shown when an individual is able to locate objects that have been invisibly displaced). Based on this framework, a scale was developed by Uzgiris and Hunt (1975), which measures object permanence capacities across 15 tasks that progressively increase in difficulty and

correspond to each of the six stages. Although this scale was originally developed to test human infants, it was used by comparative researchers as well.

While birds, like humans (and other animals), show development of object permanence capacities early in life, species variation has been found in the highest level of object permanence achieved, the speed with which transitions from one stage to another are made, and the types of errors made at different levels of development. Pigeons, domestic chickens, and ringdoves fail to show full object permanence development, whereas the larger brained species, including the common hill mynah and several psittacids and corvids show strong evidence of attaining the maximum Stage 6 (Hoffmann et al., 2011; Pepperberg & Funk, 1990; Plowright, Reid, & Kilian, 1998; Shettleworth, 1998). Additional species variation has been found in the types of errors that are made in tests of the higher levels of object permanence. Piaget (1952) found that between Stages 4 and 5, infants typically make a mistake when they are faced with a particular displacement task. In this task, an individual watches as an object is hidden in one location (location A), and is then given the opportunity to retrieve it. The object is hidden once more in location A, and in full view of the subject, is subsequently moved from location A, and hidden in an alternate location (location B). Despite observing the displacement, infants under the age of 12 months commonly fail to search location B, searching instead location A (Piaget, 1952; Rathus, 2010; Smith, Thelen, Titzer, & Mclin, 1999). Although the A not B error (also known as the preservative error) has been found in non-human species, it is not universally experienced by animals that attain Stage 5 (or higher) of object permanence. While, for instance, monkeys and apes commit this error in the course of their development, dogs and cats do not appear to show the same tendency (Dumas & Doré, 1989; Gagnon & Doré, 1994; Mathieu & Bergeron, 1981; Redshaw, 1978; Spinozzi, 1989). Corvids also

show variation in this respect; developmental studies have found evidence of the A not B error in carrion crows and ravens, but not in magpies or Eurasian jays (Hoffman et al., 2011). Thus far, psittacine research seems to indicate that the A not B error may be characteristic of parrot cognitive development (e.g., African greys, Illiger mini macaw, parakeet, and cockatiel; Pepperberg & Funk, 1990).

The significance of the A not B error, whether in terms of individual development, or species differences, is debated. It has been suggested that it may be due to an individual perceiving the object as being ‘an integral part’ to the original location, lacking the understanding that the object has ‘its own existence;’ others have argued that it is caused by an immature or underdeveloped working memory system (Pepperberg & Funk, 1990). More recently, the potential role of other executive function processes have come under focus, with authors suggesting that a lack of inhibitory control or task-switching abilities may account for the A not B error (Hoffmann et al., 2011).

Inhibitory control. Inhibitory control, which is the ability to inhibit prepotent responses, has also been identified as a component of executive function (Willoughby et al., 2012). It is believed to play a significant role in the coordination of mental resources, allowing for effective problem solving (Dowsett & Livesey, 2000). The ability to withhold an automatic or impulsive response provides individuals with the opportunity to consider alternative solutions to a problem, increasing the likelihood that a correct solution is found. Inhibitory control is therefore believed to be associated with behavioural flexibility (Amici, Aureli, & Call, 2008).

In avian species, this capacity has largely been investigated through the use of serial reversal learning and delayed gratification tasks (see Chapter 5 for a more

detailed discussion). In the former, operant conditioning is used to train subjects on discrimination tasks; once subjects become proficient, meeting criterion, reward contingencies are reversed. Individuals who are able to more quickly adapt to the new condition, inhibiting previously reinforced responses, are considered to have inhibitory control capacities (Kralik, Hauser, & Zimlicki, 2002). In delayed gratification tasks, subjects have to inhibit the response of reaching for a small quantity of food immediately available in order to obtain a larger quantity of food at a later point (Vick, Bovet, & Anderson, 2010). Such research has yielded evidence of inhibitory control capacities among birds, with performance on inhibitory control tests varying across species.

As has been the case with other cognitive capacities, associations have been identified between performance on inhibitory control tests and measures of social complexity and brain size (Amici, Aureli, & Call, 2008; Bond, Kamil, & Balda, 2007; Maclean et al, 2014). Research comparing three North American corvid species, for instance, reported that the pinyon jay, the species with the greatest social complexity, showed the strongest behavioural flexibility in serial reversal learning when compared with less social corvids (Bond et al., 2007). Comparative research has also found greater inhibitory control capacities among magpies and yellow headed parrots, as compared to the smaller-brained chicken and quail (Gossette, Gossette, & Riddell, 1966). Similarities in corvid and parrot performance are also seen in delayed gratification tasks. In separate studies, Goffin's cockatoos and two types of corvids (crows and ravens) were found to significantly delay consumption of readily available food for a preferred reward, showing preference for food quality over quantity (Auersperg, Laumer, & Bugnyar, 2013; Hillemann, Bugnyar, Kotrschal, & Wascher, 2014).

These findings, including those obtained through object permanence research, provide evidence of executive functions in birds, including working memory, inhibitory control, and perhaps task switching abilities. Thus, it appears that at least some avian species possess cognitive skills that are fundamental to flexible problem solving. However, to gain a true understanding of the nature of physical problems, one must have conceptions about the physical world.

Concept formation. Referred to as the “building blocks of thought”, concepts allow individuals to organize their experiences and connect previously acquired information to new circumstances (Hockenbury & Hockenbury, 2015, p. 273). Concept formation relies on the process of categorization, which makes it possible for generalizations and distinctions to be made between classes of objects or abstract ideas. The ability to organize information in this manner, it has been argued, brings order to one’s mental life and makes it possible for one to perceive the world as being stable (Roberts, 1998; Wright, 1991; Zentall, Galizio, & Critchfield, 2002). Concepts therefore aid individuals in identifying, and perhaps understanding, the general principles that underlie and connect different types of problems and problem solving strategies.

The capacity to generalize stimuli within a given category and/or discriminate stimuli in different categories, has been found in a variety of avian species, including small-brained birds (Herbranson, Fremouw, & Shimp, 2002 ; Pepperberg, 1987; Smirnova, Lazareva, & Zorina, 2000; Werner & Rehkämper, 2001; Zentall & Hogan, 1978). Chickens have been found capable of categorizing multidimensional geometrical figures (Werner & Rehkämper, 2001), and pigeons have shown competency in tasks that required them to categorize moving stimuli according to

speed, direction, or both (Herbranson et al., 2002). High performance on such tasks, however, does not necessarily provide evidence of the acquisition, or use, of concepts; subject performance may be based on the memorization of a set of rules specific to stimuli features and/or configurations used during trials. Various studies therefore include transfer tests that consist of novel stimuli, but can be solved with the same general rule (e.g., pick the smallest stimulus in the array) as was used during earlier (training) trials. If subjects show competent performance in the first few trials of transfer tests, this indicates they acquired and applied the general rule (Cook, Katz, & Cavoto, 1997; Pepperberg, 1987; Shettleworth, 1998; Smirnova et al., 2000).

Researchers distinguish between concrete concepts (based on the grouping of perceptually similar objects, e.g., plants, stones) and concepts that require higher forms of abstraction, such as relational concepts (e.g., 'smaller than,' 'different than,' 'equal to;' Zorina & Obozova, 2012). The latter is considered to be an example of a highly advanced mental process, and is believed to be rare in the animal kingdom (Smirnova, 2011; Zorina & Obozova, 2012). In tests of transfer, pigeon performance indicates the capacity for concrete concept acquisition. For example, pigeons have passed tests requiring the discrimination of images that contained people from images that did not (Hernstein & Loveland, 1964). It is at the more abstract level, that pigeons begin to show the limits of their concept acquisition capabilities. Although some studies report successful transfer of same-different tasks by pigeons, subjects generally require an extensive amount of training to reach criterion (e.g., approximately 3,000 trials; Cook et al., 1997) and do not show immediate transfer (Cook et al., 1997; Katz & Wright, 2006). Furthermore, studies have found significant differences in pigeon performance depending on research methodology.

Failure to find convincing evidence of abstract concept acquisition in pigeons is not particularly surprising given that comparative studies have identified associations between avian concept acquisition and brain complexity (Emery, 2006; Smirnova, 2011; Zorina & Obozova, 2012). Crossbills and ravens, for instance, have been found to outperform gulls in relational tasks (as predicted by species differences in brain complexity; Benjamini, 1983; Zorina & Obozova, 2012). Thus far, the most compelling evidence of the ability to acquire relational concepts has been found in corvid and psittacine research. Smirnova et al. (2000), for example, report the successful transfer of the oddity concept to new stimuli by crows. Subjects were given a series of oddity-from-sample problems, with stimuli varying according to three different categories: shape, colour, and number of items in a display; all of the crows that passed training (4/6) showed transference of the oddity concept in all categories. Similarly, an African grey parrot was trained to identify differences and similarities among various objects, and was tested for transference (Pepperberg, 1987). As the subject had the capacity to vocalize human speech and had been previously taught to use vocal labels (e.g., 'shape,' 'colour,' 'material'), the experiment tested the parrot's ability to correctly answer questions such as, 'What is different?' and 'What is same?' when presented with an assortment of objects. The results are persuasive (85% correct on tests using novel objects), indicating a comprehension of the same-different concept.

Evidence of abstract concept formation in corvids and parrots gives one reason to believe that their understanding of the physical world may indeed be complex, and that they may be able to reason about physical objects and the unobservable forces that act on those objects. This understanding is often referred to as 'folk physics' (Silva et al., 2005).

‘Folk physics’ and understanding causality. Visalberghi and Tomasello (1998) define causal understanding as the recognition of a mediating force (e.g., gravity) that binds two events together, which can be used to predict or control those events. Conceptions of causal forces, for instance, make it possible for individuals to understand how objects interact together and how they can be manipulated to produce a desired result. Thus, when a novel problem is encountered, general principles of causality can be used to quickly identify connections between the physical properties of a task and effective solutions; this is far more efficient than trial and error learning, and allows for more flexibility than associative learning (Krasheninnikova, Bräger & Wanker, 2013).

Insightful problem solving, which is defined as “the sudden arrival of the solution to a problem,” has been identified as an indicator of causal understanding (Foerder, Galloway, Barthel, Moore & Reiss, 2011, p. 1). Some of the earliest experimental investigations of avian cognition focused on this capacity, measuring the competency of various species to solve novel string pulling tasks (Thorpe, 1956; Vince, 1956, 1958, 1961). A number of small passerine species (including tits and finches) were presented with a single baited string hung vertically from a perch. The birds were tested to see if they would spontaneously employ the correct solution (grabbing the string with the beak, securing it under foot, repeating actions until the food is obtained) the first time they encountered the problem. While most subjects were found capable of solving the task, comparative analyses showed that successful performance in this task could be explained by species’ innate feeding patterns. The species that showed the highest performance (solving the task within the first trial) had a natural tendency to use their feet during feeding (e.g., great tits); those that did not share this trait (e.g., canaries) demonstrated significantly more trial and error learning (Vince, 1956, 1958,

1961). As a result of these findings (and similar findings from subsequent research), string-pulling paradigms have been developed that more robustly test birds' 'folk physics'. Evidence of insightful problem solving has been found among corvids and psittacines. Heinrich (1995), for instance, tested ravens on three simultaneous choice tests; each test presented subjects with two strings hung in close proximity to each other, and string configurations varied in each test (Test 1, one string was baited with food and the other with a rock; Test 2, strings were crossed; Test 3, a novel string was baited and the familiar string was not). Although within species variation was found, some of the ravens showed immediate and consistent high performance in all tests. These birds selected the correct strings at levels significantly above chance upon initial exposure to tests. As these ravens' performance was immediately high, Heinrich concluded that their problem solving was more likely explained by insight than by discrimination learning, and thus perceived a means-end relationship between the food and string. Subsequent research provided further support for the notion that causal understanding serves as a viable explanation for the ravens' performance (Heinrich & Bugnyar, 2005).

In a study that was inspired by Heinrich's research, Werdenich and Huber (2006) tested seven captive-born keas naive to the string-pulling paradigm; they were presented with four tests, including object discrimination, crossed strings, slanted strings, and overload tasks. In the overload test, one string was attached to a baited cup, and the other was attached to a large rock covered in butter (a valued food item). As the rock was far too heavy to be pulled up, this task probed subjects' understanding of weight. Lastly, flexibility in problem-solving was tested in an overlength test (a baited string was presented that was so long that the food could be easily obtained from the ground). Performance was found to be high (80 % correct or higher in the first 10

trials) in the object discrimination and slanted string tasks; a high degree of variation was found in the overload task, and poorest performance was found in the crossed string and overlength tasks. The authors suggest that while goal directed behaviour was demonstrated by the parrots, poor performance on the crossed string and overlength tasks indicates that it is unlikely that the birds relied upon insight to solve the object discrimination and slanted string tasks.

Hyacinth and Lear's macaws have also shown difficulty with the crossed strings condition, despite high performance in other conditions (including a pair of strings with one baited and the other empty, and a pair of strings with one connected to food and the other near food, but not connected to it; Schuck-Paim, Borsari, & Ottoni, 2009). Although the macaws failed to perform significantly above chance in the crossed strings condition, their high performance on the other tests is noteworthy (significantly above chance in the first seven trials), as researchers controlled for weight and movement to minimize perceptual cues that subjects could use to identify the correct string. Interestingly, while ravens, keas, and macaws have performed poorly on crossed strings tests, spectacled parrotlets, which are among the smallest parrot species, have been perform competently on tests that use this configuration (performing significantly above chance in 25 trials, Krasheninnikova et al., 2013). Although research on macaws and parrotlets provide reason to believe that causal understanding may be a feature of psittacine cognition, it is unclear how common it is throughout the order. Other species, such as green-winged macaws, sulphur-crested cockatoos, and blue-fronted Amazons, have failed to show understanding of means-end relationships in string pulling discrimination tasks (Krasheninnikova et al., 2013; Schuck-Paim et al., 2009); it should be noted, however, that sample sizes in these studies were quite small, so these results may not be representative of the species.

While string pulling research can yield valuable information about species' problem solving capacities, findings can often be difficult to interpret as some species show high performance on some tests (e.g., tests of connectedness), but not others (e.g., crossed strings tests). Investigating tool use provides an alternate method of exploring causal understanding. Although tool use has been documented in the wild in a variety of birds, the number of species that have been systematically investigated under controlled conditions is relatively limited.

Interestingly, one of the earliest accounts of spontaneous and flexible tool use by a bird in a laboratory setting is of a species that is not known for being a natural tool user. In a study of captive-reared Northern blue jays, Jones and Kamil (1973) describe a subject's use of a piece of newspaper to rake food pellets into its cage after it experienced a period of food deprivation (pellets that could not have otherwise been accessed). The bird was documented engaging in various types of manipulation of this material, such as shredding or crumpling it before using it. On some occasions, the jay was even seen placing the paper in its water dish before sticking it through the wire of its cage to 'mop up' small food particles, which would be consumed once the bird pulled the wet paper back into its cage.

Amongst the natural tool users, New Caledonian crows have been some of the most thoroughly studied in controlled experiments that aimed to determine whether they understood the unobservable forces that make tools effective. In the wild, these birds have been found to modify materials to extract prey, including the creation of hook-shaped twigs and 'stepped-cut' pandanus leaves (Hunt, 1996). Field studies have provided evidence of their capacity to flexibly respond to foraging tasks, as they have been found to make finely tuned adjustments to the objects they use to make them more effective (Hunt & Gray, 2003, 2004). In a number of experimental studies, crows have

shown the capacity to select the most appropriate tool for a given task when presented with an array of items with varying features (e.g., length or diameter); they have also been found capable of shaping unfamiliar materials to create effective tools, and have shown the ability to use one tool to manipulate another tool (meta tool task) (Chappell & Kacelnik, 2002, 2004; Taylor, Hunt, Holzhaider, & Gray, 2007; Weir, Chappell & Kacelnik, 2002; Weir & Kacelnik, 2006).

Findings from crow studies can be contrasted with those obtained from research on another natural tool user, woodpecker finches. These birds, like New Caledonian crows, use plant material (cactus spines and twigs) to extract otherwise inaccessible prey (Tebbich, Taborsky, Fessl, & Blomqvist, 2001). In a study on wild-caught birds, Tebbich and Bshary (2004) presented finches with three types of tests that included trap-tube, tool length choice, and tool modification tasks. While task acquisition was possible for all subjects after a great deal of experience with the tasks, initial responses did not provide evidence of insightful problem solving or causal understanding. Tebbich and Bshary conclude that while tool use in the woodpecker finch should not be considered a “stereotypic behavioural pattern,” as it can be modified through learning, it does not appear to involve mental representations; they state that no evidence was found that subjects had the capacity “to assess problems in advance” (pg. 696). Thus, while species may show similarities in their use of tools in the wild, the cognitive processes that underlie these foraging patterns may differ significantly between species.

One of the more intriguing findings that have emerged from avian tool use research is the impressive performance rooks have shown on a variety of tool tasks, despite the fact that this corvid species is not a natural tool user. In a series of tests run by Bird and Emery (2009a,b), rooks learned to drop a stone into a tube to collapse a tray baited with a worm. In a novel set up, a stick was presented rather than a stone; all

subjects showed immediate transfer, dropping the stick into the apparatus upon first exposure to the task. Rooks also showed the capacity to select functional tools over non-functional ones on the first trial, and had high performance on tool manufacture and modification tasks. Particularly noteworthy is their performance on a meta-tool task; on the first trial, all subjects spontaneously used a large (non-functional) stone to obtain a smaller (functional) stone, which they then used to collapse a baited platform. Based on impressive performance in this range of tasks, Bird and Emery concluded that the rooks showed evidence of insight and causal understanding. However, it should be noted that rooks have demonstrated difficulty on trap-tube tests (Tebbich, Seed, Emery, & Clayton, 2007); although they were found capable of acquiring the task, no evidence of their ability to represent key aspects of the task was found on transfer tests.

As compared to corvid research, systematic research on parrot tool use capacities is far more limited. Despite showing great skill at manipulating objects due to their foot dexterity and well developed foot-bill coordination (Forshaw, 2006), tool use does not appear to be a component of most parrot species' natural behaviour. Notable exceptions include hyacinth macaws, greater vasa parrots and goffin's cockatoos. Hyacinth macaws have been observed using leaves and pieces of wood to 'as aids' while cracking hard nuts (Borsari & Ottoni, 2005). Detailed observations of this behaviour in captivity suggest the role of learning in the acquisition of this behavior; however, it is also unclear what, if any, cognitive skills may be involved. More recently, captive vasas were found to use pebbles and date pits as grinding implements or as wedges to break off parts of seashells for consumption (Lambert, Seed, & Slocombe, 2015). Finally, a single captive Goffin's cockatoo was observed using a stick to 'rake in' a play object (a pebble) it dropped out of its cage and therefore out of reach (Auersperg, Szabo, von Bayern & Kacelnik, 2012). After seeing

the bird do this during a bout of exploratory, or play behaviour, Auersperg and colleagues provided further opportunities for the cockatoo to repeat the behaviour. It is reported that the subject used 10 different tools in 10 trials, manufacturing and modifying most. Additionally, the authors report that when they tested two other Goffin's cockatoos, the parrot that had been exposed to the first subject's tool use, also used tools, while the other cockatoo that had not had this experience did not. This study showed a clear capacity for effective and flexible object manipulation in a goal-directed manner in another non-tool using avian species. However, it is necessary to note that the role that previous experience played in this case is not known. Conclusions regarding whether or not the solution employed by the first subject was truly insightful therefore cannot be drawn.

Parrots have also been tested using the trap tube paradigm in order to test physical cognition. As was the case in Tebbich et al.'s (2007) rook study, subjects were given access to a trap tube that contained a pre-inserted rake. This was done in consideration of the fact that the parrots under investigation - six keas, three green-winged macaws, and yellow-crested cockatoos - were not natural tool users (Liedtke, Werdenich, Gajdon, Huber, & Wanker, 2011). To further address this issue, they included an altered trap tube that allowed subjects to reach into the tube and directly move the reward to either end of the tube using their bills. Overall, the birds showed poor performance, failing to respond at above chance levels in the rake and non-rake conditions (after 'cheating' was controlled in the non-rake condition). When considering the parrots' performance as compared to corvid performance in trap-tube tasks, Liedtke et al. acknowledge the major differences in task acquisition. They cite possible explanations – food storing birds may be more likely to visually track the movement of food items, and better able to use this visual feedback; it may also be that

despite similarities in brain size, the major differences psittacines show in neuroanatomy associated with vocal pathways may be linked to cognitive differences that affect problem solving abilities.

Although it is evident that innate traits (e.g., natural feeding patterns) and associative learning processes are involved in avian problem solving capacities, there is also sufficient evidence to suggest that some birds, particularly large-brained species, use cognitive processes when applying solutions. Further evidence of this comes from investigations of corvid and psittacine social cognition.

Solving problems in a social environment

As noted earlier in this chapter, the cognitive capacities that birds have demonstrated in physical tasks are also useful when it comes to processing, and responding to, social information. Although avian problem solving in a social context has not been as extensively studied as has physical task acquisition under solitary conditions, there is evidence to suggest that some species have the capacity to use social information to solve problems. The following discussion provides a brief overview of findings associated with social learning and cooperative problem solving (see Chapter 6 and 7 for more detailed discussions of these topics).

Social learning. The ability to acquire information through exposure to conspecific behaviour is one of the social cognitive capacities that have been most widely investigated in a range of avian species. The puncturing of bottle foil caps by blue tits to gain access to milk was one of the earliest documented examples of innovative behaviour that is believed to have spread through social transmission (Fisher & Hinde, 1949). This conclusion was supported in subsequent research of captive and wild tits; naive birds were found to acquire novel foraging techniques seeded in their

groups by trained demonstrators, and among the wild birds, the behaviours were found to be stable over two generations (Aplin, Sheldon, & Morand-Ferron, 2013; Aplin, Farine, Morand-Ferron, Cockburn, Thornton, & Sheldon, 2015). Observations of wild New Caledonian crows have also provided evidence of the vertical transmission of pandus leaf tool design (Holzhaider, Hunt, & Gray, 2010; Hunt, 1996). Although the ability to acquire information through social influence appears to be widespread among avian taxa, variations have been found in the complexity and type of social learning different species engage in.

Evidence of stimulus or locale enhancement has been found in a range of avian species. Considered a relatively basic form of social learning, stimulus/locale enhancement occurs when an observer's attention is drawn to a particular area or object due to the presence of another individual, affording them the opportunity to learn something valuable about the area/object (Caldwell & Whiten, 2002). Field experiments of cross-fostered blue and grey tits, for instance, have provided evidence of the social transmission of foraging sites across generations (Slagsvold & Wiebe, 2011). Investigations of pecking preferences in chickens also yield evidence of locale and stimulus enhancement (Bartashunas & Suboski, 1984). In a study of captive greylag geese, subjects that were shown (by human demonstrators) where and how to open a baited container were significantly more likely to explore the container latch than control birds; they also learned to open it through trial and error, whereas control birds did not (Fritz, Bisenberger, & Kotrschal, 2000). Similarly, magpie-jays and keas who were exposed to trained demonstrators were more likely to open a baited testing apparatus than subjects in control groups (Huber, Rechberger, & Taborsky, 2001; Langan, 1996). In a simple-choice task (baited versus non-baited cups), African greys and jackdaws were significantly more likely to select the cup most recently handled by

experimenters during test trials, even when they had been shown that the cup was empty (and thus the wrong choice, Mikolasch, Kotrschal, & Schloegl, 2012). In ravens, associations have been found between stimulus enhancement and social relationships; observers were significantly more likely to manipulate target objects (objects demonstrators manipulated) when the birds they observed were their siblings (Schwab, Bugnyar, Schloegl, & Kotrschal, 2008). As these findings indicate, stimulus/locale enhancement has been identified in both small and large brained birds.

Passerines and psittacines have also exhibited evidence of emulation, which occurs when an individual gains information about the function of an object in their environment or the goal of another's interaction with an object. In such cases, an individual's attention may first be drawn to an object because of another's activity with it (stimulus enhancement), but they then crucially learn about the outcome of a demonstrator's manipulation of the object and the affordances of the object (Caldwell & Whiten, 2002; Heyes & Saggerson, 2002). In their study of tool use in Goffin's cockatoos, Auersperg and colleagues found evidence of emulation; although they did not replicate observed patterns of tool use, subjects that were exposed to a trained demonstrator were significantly more likely to show successful tool use than subjects in a ghost condition (Auersperg, von Bayern, Weber, Szabadvari, Bugnyar, & Kacelnik, 2014). Using a two-action/two-object test, Campbell and colleagues found compelling evidence of more complex social learning capacities in European starlings (Campbell, Heyes, & Goldsmith, 1999). Subjects were tested using a baited box that contained a lid with two holes; each was obstructed by a distinctly coloured plug which could be removed by pulling or pushing. After observing trained demonstrators, subjects were found to remove the same coloured plug in the same manner as the individuals they observed. Similar findings were reported in study of budgerigars (a small parrot

species), using the same type of testing apparatus (Heyes & Saggerson, 2002). In both studies, the authors suggested that in addition to emulation, the starlings' and budgerigars' performance may be indicative of the capacity to imitate (response learning, involving the copying of behavioural patterns that have been observed, Tennie, Call, & Tomasello, 2006). Byrne (2003), however, has argued that caution should be taken when interpreting such results, as response facilitation (the priming of responses that are already part of an individual's behavioural repertoire) may provide an alternate explanation.

Some of the strongest evidence of imitative capacities in birds comes from studies of psittacine vocalizations. In general, parrots demonstrate social influences on vocal learning throughout life and across sexes (Bradbury, 2004). Various species have been the subjects of experimental investigations of vocal imitation. Rowley and Chapman (1986), for example, found that galah offspring that were fostered by Major Mitchell cockatoos adopted the majority their foster parents' calls. Experimental research has also found that male budgerigars modified their own contact calls to match those of mates they were randomly paired with (Hile, Plummer, & Striedter, 2000). Thus far, Amazon and African grey parrots have been identified as showing the most impressive range of vocal mimicry of a wide variety of sounds, including human speech (Bradbury, 2004; Cruickshank, Gautier, & Chappuis, 1993; Pepperberg, 2006). Moore (1992), for instance, reported that after repeated exposure to a human experimenter producing specific sequences of words accompanied by actions, a captive African grey replicated these sequences, despite the absence of food or attentional reinforcement.

As the above discussion illustrates, there is substantial reason to believe that social learning processes are features of avian cognition. The social transmission of

behaviour through stimulus/locale enhancement appears to be well established across a range of species; strong evidence of motor emulation (and possibly imitation) has been found in passerines and psittacines, with psittacines demonstrating impressive imitative capacities in the vocal domain.

Cooperative problem solving. Like social learning, evidence of cooperative behaviour has been observed in a range of wild animals, including birds (Cheney, Moscovice, Heesen, Mundry, & Seyfarth, 2010; Foster, 1985; Langergraber, Mitani, & Vigilant, 2007; Ligon, 1983; Möller, Beheregaray, Harcourt, & Krützen, 2001; Packer & Pusey, 1997; Sachs, Mueller, Wilcox, & Bull, 2004). However, the extent to which individuals understand the roles they and their partners play in achieving desired outcomes is relatively understudied. This is particularly true for birds. As avian taxa are largely characterized by breeding systems that involve bi-parental care, the ability to coordinate behaviour has significant fitness implications; controlled studies of breeding cockatiel pairs has provided support for this assertion (offspring survival was positively correlated to levels of synchrony and coordination mates demonstrated; (Spoon, Millam, & Owings, 2006). For species that engage in high-quality, long term partnerships, the ability to cooperate with a mate may be particularly important. As indicated in Chapter 1, it has been suggested that this trait, which is common among psittacines and corvids, may have played a significant role in the cognitive adaptations observed in these birds (Emery, Seed, von Bayern, & Clayton, 2007).

Thus far, few avian species have been the subject of experimental studies investigating cooperative problem solving. However, initial findings indicate that while corvids and psittacines may have the capacity to synchronize their behaviour with conspecifics to solve problems, they may not have an appreciation for their partners' roles in the cooperative tasks. This is supported by research using the loose

string task; ravens, rooks, and African greys were found to perform well in the simple test condition (partners were given simultaneous access to string ends), but did poorly in the delayed (one partner was given access to strings before the other partner) and apparatus choice conditions (one could be obtained by a single individual, the other required a partner) (Massen et al., 2015; Péron, Rat-Fischer, Lalot, Nagle, & Bovet, 2011; Seed, Clayton, & Emery, 2008). Péron et al. (2011) also tested African greys using a task that required complimentary actions (each partner had to engage in different behaviours in a coordinated manner); consistent with their performance on the other tests, the birds learned to engage in the appropriate actions when given simultaneous access to the apparatus, but failed to do so in the delayed condition

These initial findings indicate that while various avian species have developed the ability to synchronize and coordinate behaviour in a manner that supports a cooperative breeding relationship, it is unlikely that they have understanding of how their interactions related to specific outcomes. Clearly though, far more research has to be conducted in this area of study, including the number of species studied and developing additional test paradigms

Conclusion

Although relatively few avian capacities have been the focus of thorough cognitive investigation, preliminary findings suggest that some birds possess cognitive adaptations that allow for flexible problem solving. On physical tasks, birds have shown evidence of working memory, inhibitory control, concept formation, and potentially causal understanding (Benjamini, 1983; Bird & Emery, 2009a,b; Bond et al., 2007; Heinrich & Bugnyar, 2005; Hoffmann et al., 2011; Hunt & Gray, 2004; Pepperberg, 1987; Pepperberg & Kozak, 1986; Seed et al., 2006; Smirnova et al., 2000; Zentall et al., 2002). Birds have also demonstrated social learning capacities, including

imitation (Campbell et al., 1999; Heyes & Saggerson, 2002; Hile et al., 2000; Moore, 1992; Pepperberg, 2006). However, species variation observed in task performance indicates that the capacities corvids and psittacines possess are relatively complex among avian taxa. This assertion is not only supported by cognitive research findings, but also by the positive correlations that have been found between brain size and mental capacities (Emery, 2006; Emery et al., 2007; Lefebvre, Nicolakakis, & Boire, 2002; MacLean et al., 2014; Zorina & Obozova, 2012). In Chapters 5, 6, and 7, I present original research findings aimed at furthering our understanding of psittacine physical and social cognition.

CHAPTER 3: STUDY SPECIES

The observational and experimental research presented in this thesis focuses on two closely related species of Neotropical parrots, orange-winged Amazons (*Amazona amazonica*) and blue and gold macaws (*Ara ararauna*). These species were chosen as study subjects for several reasons. First, there is a general lack of knowledge about the psittacoidea superfamily, particularly with regards to their cognitive capacities. Most heavily studied thus far are African grey parrots, and though this research has revealed impressive cognitive potential (primarily in the areas of language comprehension and concept acquisition, Pepperberg, 1983, 1987, 1990, 1994; Pepperberg, Garcia, Jackson, & Marconi, 1995), results are based on small numbers of individuals, so it is unclear how generalizable findings are within this species and even less clear how pervasive complex cognition is among the psittacoidea. There are over 300 species that make up the family and very little is known about the majority of them beyond their basic ecology (Forshaw, 2006). It is therefore clear that far more research is needed before conclusions can be drawn about the degree to which complex cognition is characteristic of the ‘true parrots.’ My research into two psittacoidea species, of which little is known, aims to further our understanding of behaviour and cognition in this family of parrots.

Second, orange-winged Amazons (OWAs) and blue and gold macaws (BGMs) were selected as research subjects due to key species characteristics. These closely related species inhabit the same ecological environment and share the same social organizational patterns, however crucially for this project there are indications of differences in the quality of the partnerships they form. Specifically, anecdotal reports of captive birds suggest that BGMs develop more intense bonds with their partners than

OWAs, with macaws spending more time engaging in affiliative behaviours with their partner and showing little interest in, or tolerance of, other conspecifics. OWAs, on the other hand, have been reported as being more likely to have several affiliative partners, or 'friends,' in addition to their main partners (Steve Nichols, personal communication). I aimed to first validate these anecdotal reports by collecting systematic observational data on partner relationship quality. If OWA and BGM are shown to differ in their relationship quality, this will allow meaningful between species comparisons of cognitive skills that will be relevant to examination of the Relationship Intelligence Hypothesis (proposed by Emery, Seed, von Bayern, & Clayton, 2007); see Chapter 1 for a review of this hypothesis). The following section provides a summary of what is currently known about OWA and BGM socio-ecology, and reviews the limited behavioural and cognitive experimental research published on the two species.

Natural History

OWAs and BGMs belong to the same Tribe (Arini), which split from the psittacoidea superfamily 35 mya (psittacoidea diverged from their ancestral line 47 mya). The last common ancestor of Amazons and macaws is believed to have lived 25 mya (Schweizer et al., 2011). Although relatively closely related, OWAs and BGMs are physically very distinct from one another (see Figure 3.1). BGMs are one of the largest psittacine species, with adults measuring approximately 86 cm in length and weighing 1,100 g. OWAs are significantly smaller, considered a medium sized parrot; they measure approximately 31 cm in length, with an average weight of 350 g (Forshaw, 2006). BGMs also have a larger absolute brain size (18.08 ml) than OWAs (8.29 ml) (Iwaniuk, Dean, & Nelson, 2005). As can be seen in Figure 3.1, their

colouration is quite different and in both species males and females share the same colouration.

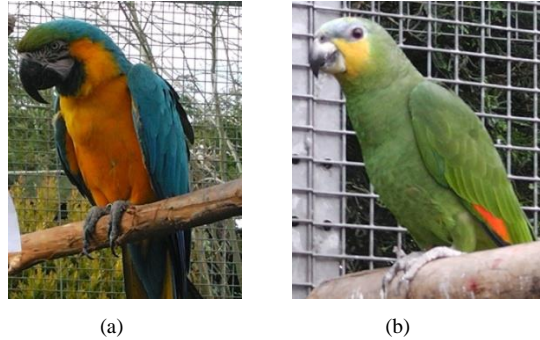


Figure 3.1. Photographs of a blue and gold macaw (a) and an orange-winged Amazon (b).

OWAs and BGMs belong to the same family (*psittacidae*) and are typical of most ‘true parrots’ in many respects. Adapted to a tropical climate, both species can be found throughout large regions of South America, including Columbia, Venezuela, and Brazil. Although they primarily live in forested or wooded habitats, some populations of both species can also be found in open or semi open savannahs. Both show preferences for wetter environments; this is particularly true for OWAs, which can often be found in mangrove swamps. As is typical of parrots, OWAs and BGMs are diurnal birds, with activity levels peaking in the early mornings and late afternoons, when they do most of their foraging. OWAs and BGMs rest and forage in the upper levels of tree canopies, feeding on fruits, seeds, and nuts (Forshaw, 2006; Hoppe, 1992; Luescher & Luescher, 2006). Though both species prefer to rest and forage high in tree tops, BGMs regularly forage on the ground as well, an activity that is rarely seen in OWAs. These birds are long-lived animals, with estimated life spans varying, but falling in the range of being between 35 to 60 years (Brouwer, Jones, King, & Schifter, 2000). Although these parrots commonly occur in large numbers throughout the

regions they inhabit, their populations are under increasing pressure due to loss of habitat and demands from the pet trade (Forshaw, 2006).

Socio-ecology

Highly social species, OWAs and BGMs have both been described as ‘gregarious, noisy, and conspicuous’ (Forshaw, 2006). They demonstrate similar social organizational and activity patterns. Both species congregate in the largest groups at midday or night time communal roosts. These large flocks emit loud and frequent vocalizations, with call intensity generally peaking early in the morning as roosting birds prepare to break up into smaller foraging parties; vocalizations also increase as foraging groups return to roost (Forshaw, 2006; Hoppe, 1992). OWA communal roosts tend to be very large, with some consisting of hundreds of individuals, whereas macaws tend to roost in groups of about 20 to 40 (Forshaw, 2006; Hoppe, 1992; Pitter & Christiansen, 1997). The greatest numbers of macaws have most often been recorded at clay licks, which are favoured foraging sites that can attract over 100 individuals of various macaw species (Brightsmith, 2004). Group sizes tend to vary for OWAs and BGMs depending on the season, with larger group sizes more commonly seen outside the breeding season than during it (Forshaw, 2006). In general though, BGMs travel in smaller groups, with pairs being easily discernible due to their close proximity and synchrony during flight (Forshaw, 2006). In BGM and OWA societies, bonded pairs (usually mated pairs) are the most stable social components. As is the case with most psittacines, these species are monogamous and maintain their partnerships all year round. They are believed to mate for life, with pairs cooperating in the protection of resources, defence against predators, and the rearing of their young (del Hoyo, Elliott, Sargatal, & Cabot, 1992; Hoppe, 1992).

Breeding. In BGMs, sexual maturity is reached at approximately five years of age, and in OWAs, at three to four years (Hoppe, 1992; Sullivan, 2013). Both parrots show similar patterns of behaviour as seasons change. As the breeding season approaches, pairs split off from communal roosts; they take ownership of nest sites and become increasingly less tolerant of conspecifics. A difference is seen, however, in the degree of intolerance expressed by these species. BGMs are known to be extremely hostile towards individuals that approach their nest sites, directing high levels of aggression towards any bird that comes within 100 m of nests (Renton, 2004). A lower density of breeding pairs is therefore seen in BGMs nesting sites, as compared to OWAs (Luescher & Luescher, 2006; Renton, 2004). Like the majority of *psittacoidea*, OWAs and BGMs are cavity nesters, both preferring to nest in dead palms. OWA pairs tend to produce more fledglings per breeding season than BGMs. While BGMs have a clutch size of two to three eggs, OWAs generally lay three to four. Chick survival rate tends to be low in both species (approximately 50% or lower) due to predation, nest site competition, and poaching (Brightsmith & Bravo, 2006; Forshaw, 2006; Hoppe, 1992; Millam, Kenton, Jochim, Brownback, & Brice, 1995).

These parrots engage in bi-parental care until chicks fledge at approximately 60 days. Fledglings remain with their parents for several months afterwards, travelling with them to foraging sites and communal roosts. This is believed to be a critical learning period, not just with regards to learning about food sources, but also with regards to socialization (Brightsmith & Bravo; 2006; Hoppe, 1992). Highly social creatures, these birds require access to conspecifics with which they can bond. This is evidenced by the maladaptive behaviour that is often demonstrated by captive parrots, which are often kept in isolation (Meehan & Mench, 2006).

In Captivity

Pet Trade. Both OWAs and BGMs are kept as pets, with OWAs being among the most commonly bought and sold parrot in captivity (Hobbe, 1992). Because of their beauty and ability to mimic human speech, these birds are popular and highly valued. These wild species, however, are challenging to maintain as pets. Because of this, a large majority of them are re-homed several times throughout their lives, which is very common for the larger parrot species kept as pets (Meehan & Mench, 2006). A contributing factor to this is their destructive nature. Pet birds allowed to spend time outside their cages will often cause significant damage to furniture. Their powerful beaks can also cause severe injuries to pet owners, particularly when it comes to BGMs. An additional drawback of macaw and Amazon parrot ownership is the level of noise one has to tolerate. They regularly vocalize loudly and for prolonged periods of time throughout the day. It is also commonplace for parrots housed alone to develop significant maladaptive behaviours, such as feather plucking or other types of compulsively repetitive behaviours known as stereotypies (Meehan, Garner, & Mench, 2003). These signs of stress often become too much for owners to contend with. Unfortunately, these challenges cause the frequent re-homing of these animals and contribute to the neglect that many captive parrots experience (Meehan & Mench, 2006).

Because these problems are so widespread and the demand for parrots in the pet trade remains high, it is not surprising that for some species more research has been conducted on their welfare than on their cognitive capacities. OWAs provide an example of this, having more often been subjects in experimental investigations examining the development of abnormal behaviours than subjects in cognitive studies.

BGMs, on the other hand, are essentially absent in literature reporting captive behavioural and cognitive research; instead, they have most often been subjects of veterinary articles focusing on the occurrence and treatment of psittacine diseases and infections.

OWA research. Although little is known about OWA cognition, much has been determined about the environmental conditions under which these parrots are likely to develop maladaptive behaviours. Results among experimental studies are consistent, producing clear evidence of their need for physical and social enrichment. Researchers compared OWAs housed in barren cages to those housed with toys and given access to enrichment opportunities. As would be expected, parrots in the former group were found to be significantly more likely to develop stereotypies (Meehan, Garner, & Mench, 2004). Physical enrichment alone, however, is not sufficient for normal behavioural development. In another study conducted by the same researchers, OWAs housed alone were compared to OWAs housed in pairs. All subjects were kept in cages that provided a high degree of physical enrichment (e.g., objects they could climb on, swing on, and manipulate). They were all additionally provided with enriching foraging opportunities (e.g., extracting food from containers). Despite experiencing the same physical and foraging enrichment, behavioural differences among the two groups was highly significant. Of the socially isolated parrots, 57% developed stereotypies; in contrast, none of the paired birds did. Furthermore, the paired OWAs ‘screamed’ less, spent less time preening, and were more likely to interact with enrichment objects. They also demonstrated less fear and aggression towards unknown human handlers (Meehan, et al., 2003).

Behavioural responses to objects have also been studied in OWAs, with a focus on neophobia and object preference. OWAs are known to be neophobic birds, showing

fearful responses when encountering novel objects or individuals. This trait has been studied to determine whether intra-species variation is associated with early experience. Though it had been suggested that rearing type (hand-reared versus parent-reared) may predict severity of neophobia, experimental research provided no support for this notion. Instead, Fox and Millam (2004), argue that it is the degree of experience a chick has with novelty within the first few weeks of life that is likely to be the most significant factor predicting neophobia levels in adulthood (Fox & Millam, 2004). With regards to object preference, studies report OWAs show preferences for enrichment objects based on various features, including colour, size, texture, and hardness, that matched food items in their diets. Sex-specific differences in object preferences have also been reported (Kim, Garner, & Millam, 2009; Webb, Famula, & Millam, 2010).

It is only recently that studies on OWA cognition have been published. A series of experiments conducted by Cussen and Mench (2014a, b) measured several cognitive processes in OWAs using Hamilton search tasks (also referred to as Hamilton perseverance tasks). Originally created to test learning in mammals, and most commonly used in primate research, this paradigm involves the following: subjects are presented with four identical, opaque containers, one of which is baited. The subject's task is to locate the food reward by selecting the appropriate container. Rules used for which containers are baited may vary depending on researchers' study objectives. However, a pseudorandomized procedure is generally used, wherein the reward location is chosen randomly with one constraint – the same container is never baited on consecutive trials. In such a test, a subject's optimal response would therefore include avoidance of the container baited in the previous trial; selecting the previously baited container would thus be counted as an error.

The procedure described above was used by Cussen and Mench (2014a) in an initial phase of OWA testing. In a second phase, the authors changed learning set requirements in order to test OWA cognitive flexibility. In this condition, the reward location was fixed. Parrots were therefore measured on their ability to break the previously acquired strategy with the pseudorandomized set, and switch to the optimal one of immediately selecting the same (baited) container on each test trial. In Phases 1 and 2, trials lasted 2 min and subjects were allowed to make multiple choices during that period. In a third testing phase, subjects were restricted to one choice per trial (the reward location was the same as in the previous phase).

The authors report that OWAs demonstrated the capacity to solve the Hamilton search task using trial and error learning, although they demonstrated side preferences. Cussen and Mench found no evidence that they acquired the optimal strategy in the initial phase –avoiding the previously baited container. The authors argue, however, that the birds demonstrated flexibility in Phase 2, as the average number of choices they made decreased across trials within the first test session. Furthermore, when OWAs were restricted to one choice per trial (Phase 3), they showed immediate significant improvement. Based on this finding, Cussen and Mench conclude that motivational factors may have played a larger role in OWA performance than cognitive factors. OWAs also showed evidence of task retention when tests were repeated six months later. The authors additionally report a significant degree of individual variation in performance in the initial phase; OWAs with strongest motor lateralization (foot preference) performed better than those with less lateralization. Cussen and Mench report that this is consistent with previous findings of other species tested on this task, suggesting an association between lateralization and cognitive capacity.

The Hamilton search task was used by Cussen and Mench (2014b) in a subsequent study to further investigate individual variation in OWAs. The authors found significant intra-species differences in attention bias while completing the task, which were predicted by ‘personality’ assessment measures. Two raters independently scored subjects on 36 traits (e.g., boldness, alertness, sociability) over the period of a week to identify stable characteristics. Parrots that scored higher on scales of Neuroticism were found to demonstrate significantly more ‘attention bias for environmental stimuli’ (tested by introducing the presence of an unknown human during test trials), which interfered with task acquisition.

These preliminary investigations into OWA cognition suggest that at the very least, this species has the capacity to engage in trial and error learning and shows evidence of flexibility in task acquisition. This research has also provided initial evidence of an association between intra-species variation in cognitive task performance and individual variation in stable behavioural traits (motor-lateralization and neuroticism) (Cussen and Mench, 2014a,b). Although these are interesting findings, they are limited in scope, with most areas of cognition under investigated. Even so, having some information is preferable to having none, which is unfortunately the case with BGMs. While several books have been written about BGM pet ownership, almost no empirical research has been published reporting controlled BGM studies.

BGM research. It has been somewhat surprising to discover that despite their prevalence in captivity, research on BGM cognition appears to be non-existent. An intensive literature search of European and American scientific journals yielded one publication of a controlled behavioural study of BGMs. Researchers compared eight BGMs and three tufted capuchin monkeys (*Sapajus paella*) in an object manipulation

study, consisting of two experiments (Brunon, Bovet, Bourgeois, & Pouydebat, 2014). The first experiment consisted of three tests; each measured the influence of a specific physical property (colour, texture, or shape) on subject preference for enrichment objects. The second experiment tested subjects' capacity for complex manipulation. Subjects were tested using two transparent (baited) boxes; one could be opened by pulling a handle; the other required the removal of a latch, followed by pulling a handle.

BGMs and capuchins performed similarly in the first experiment, interacting more frequently with objects that resembled food items (in terms of shape, colour, or texture). Capuchins showed better performance on complex object tests, opening boxes significantly more quickly than BGMs; two of three monkeys opened the boxes, whereas only two of eight BGM did. The authors suggest, however, that neophobia may have played a role in BGM performance (they showed greater hesitancy when approaching boxes). These findings therefore provide evidence that BGMs have the capacity to solve novel foraging tasks through object manipulation. This is not surprising given the fact that macaws engage in extractive foraging in the wild (Forshaw, 2006).

Conclusion

BGMs and OWAs, like other parrots, have adapted to physically and socially complex environments. As a consequence, they demonstrate many of the traits found among highly intelligent species. These birds are large-brained, long-lived, and develop long-term partnerships; they engage in extractive foraging and rely on food sources that vary spatially and temporally (del Hoyo et al., 1992; Forshaw, 2006; Hoppe, 1992). These traits, along with what has been discovered about the cognitive capacities of other psittacines, suggest the potential for complex cognition in BGMs

and OWAs. This thesis offers a contribution to psittacine research by providing an examination of problem-solving capacities in these two species. It additionally reports an observational study analysing social behaviour, with a focus on relationship quality variation. This study is the focus of the following chapter.

CHAPTER 4: RELATIONSHIP QUALITY

Abstract

This observational study investigates relationship quality in captive, flock-housed OWAs ($N = 14$) and BGMs ($N = 11$). Data were collected on affiliative (proximity, allopreening, synchrony/coordination, courtship feeding, agonistic support) and social tolerance behaviours (agonistic displays, approach tolerance, co-feeding, pilfer tolerance). Focal birds in both groups showed selective affiliative investment, showing a preference for specific flock members (preferred partners); heterosexual and isosexual focal bird-preferred partner dyads were identified. OWAs and BGMs showed similar levels of affiliative investment in social relationships, although BGMs exhibited two affiliative behaviours not observed in OWAs (vent allopreening and courtship feeding); no significant between species differences were found in focal birds' composite affiliative investment scores with preferred partners. Both species showed significantly greater tolerance of approaches by partners as compared to non-partners. However, OWAs showed higher overall levels of social tolerance towards preferred partners. Composite social tolerance and affiliative scores were not found to be correlated in either species. Between species differences were found in body regions allopreened. OWAs spent more time engaged in head allopreening than BGMs, and BGMs spent significantly more time engaged in body and vent allopreening than OWAs. Mutual allopreening was found to be positively correlated with composite affiliative scores in OWAs, but not BGMs. This study's findings show that OWAs and BGMs are socially complex, forming partnerships that are actively maintained through various forms of affiliative behaviours, and identifies potentially important between species variation.

Introduction

In order to be able to adequately address hypotheses about the evolutionary association between social and cognitive traits, more needs to be learned about the nature of the relationships that make up animals' social systems. Relationship quality has been found to explain variations in the pattern, distribution and function of a range of behaviours (within and between groups), with significant implications for individual and group fitness (Dunbar & Shultz, 2010; Fraser & Bugnyar, 2010). Assessing an individual's ability to establish and maintain cooperative relationships, for example, may predict offspring survival rates, predatory defence success, or the ability to acquire and protect resources (Möller, Beheregaray, Harcourt, & Krützen, 2001; Silk, Alberts, & Altmann, 2003; Spoon, Millam, & Owings, 2006; Treves & Chapman, 1996).

Relationship quality measures can also be used to test predictions about partnership stability and survival outcomes. In addition, such measures can be used to test social intelligence hypotheses, such as the Relationship Intelligence Hypothesis, that propose an evolutionary link between social and cognitive complexity (Bolhuis & Giraldeau, 2005; Fraser & Bugnyar, 2010). A comprehensive comparative framework is therefore needed that identifies and defines behavioural expressions of affiliative relationships in a variety of species (Dunbar & Shultz, 2007, 2010; Emery, Clayton, & Frith, 2007; van Horik, Clayton, & Emery, 2012). The observational study reported in this chapter, which explores and compares relationship quality in orange-winged Amazons (OWAs) and blue and gold macaws (BGMs), contributes to this scientific endeavour.

As discussed in Chapter 1, parrots provide a unique opportunity to explore the potential association between social and cognitive complexity. Although social

monogamy is widespread among birds, and found in various mammalian species, psittacine pair bonds stand out as prime examples of stable affiliative relationships. They have some of the most enduring relationships in the animal kingdom (some spanning decades), with partners investing a high degree of energy into actively maintaining the bonds they establish (Forshaw, 2006; Hoppe, 1992; Seibert, 2006; Spoon, 2006). This characteristic, along with evidence of cognitive complexity in the Psittaciformes order (see Chapter 2), make parrots particularly valuable when it comes to research that is aimed at exploring the ‘Relationship Intelligence Hypothesis’ (proposed by Emery, Seed, von Bayern, & Clayton, 2007).

The significant correlations that have been found among species’ brain sizes, degree of cognitive complexity, and tendency to form long-term partnerships, provide support for this assertion (see Chapter 1). These findings suggest that long-term relationship maintenance selects for behavioural and cognitive complexity (Dunbar & Shultz, 2007; Emery, Seed, et al., 2007; Shultz & Dunbar, 2010). It has been argued that the benefits obtained from pair bonding, both in terms of individual fitness and offspring survival, put pressure on individuals to invest energy into the maintenance of their partnerships. In this type of social environment, individuals that are skilled at reading and responding to mates’ social signals, and are able to effectively coordinate and cooperate with them, are more successful; this, however, is cognitively demanding and is thus believed to have selected for cognitive flexibility (Emery, Seed, et al., 2007; Shultz & Dunbar, 2010). By operationally defining features of relationship quality in large-brained, highly social, and cognitively complex animals like parrots, we can test how strongly associated relationship variables and cognitive complexity are.

The following section provides an overview of behaviours that have been identified as meaningful in the establishment and/or maintenance of affiliative

relationships in various species; research reviewed in this section provided the basis upon which I developed the relationship quality measures I used in the OWA and BGM observational study presented in this chapter.

Affiliative indicators and relationship maintenance. One of the most commonly used approaches to identifying affiliative relationships consists of tracking how often individuals are in close proximity to one another (or amount of time spent in close proximity). A tendency to be in close proximity, particularly when individuals have the option of being near other group members as well, suggests motivation to maintain physical closeness. Proximity measures have been used in numerous field studies to identify relationship stability in many species; examples include chimpanzees, baboons, spotted hyenas, lions, bottlenose dolphins, northern long-eared bats, barnacle geese and rooks (Black, 2001; Garroway & Broders, 2007; Gilby & Wrangham, 2008; Emery, Seed, et al., 2007; Möller, et al., , 2001; Silk, Altmann, & Alberts, 2006; Zabel, Glickman, Frank, Woodmansee, & Keppel, 1992). Similarly, research on wild psittacines show that spatial organization of flock members illustrate association patterns, with distances between non-mates and non-kin being significantly greater than distances between mates and kin. This is highly common among birds; however, tolerance of non-mates varies among species, as does the extent to which proximity is maintained between pair bonds throughout the year (Forshaw, 2006; Hoppe, 1992; Pitter & Christiansen, 1997; Seibert, 2006). It is argued that the primary evolutionary function of this behaviour is mate guarding, preventing competitors from copulating with mates (Bolhuis & Giraldeau, 2005). While useful, measures of proximity are limited in what they can reveal about the nature of an affiliative relationship. To more thoroughly assess relationship quality, the types of social interactions partners engage in must be closely examined. The amount of effort

individuals invest in maintaining and strengthening bonds, for instance, can be measured by looking at a range of affiliative behaviours (Shultz & Dunbar, 2010).

One of the most complex social interactions primates and birds frequently engage in is allogrooming/allopreening (when one individual grooms another; Dunbar, 1991; Dunbar & Shultz, 2010; Harrison, 1965; Lewis, Roberts, Harris, Prigmore, & Wanless, 2007; Seibert, 2006; Seyfarth, 1977). Although social grooming is believed to have initially evolved because of its parasitic control function, making it possible for individuals to have parasites removed from body regions they could not self-groom, there is abundant evidence that it serves social functions as well (Dunbar, 1991; Lewis et al., 2007; Wilkinson, 1986).

Although there are differences in the types of grooming networks species develop (e.g., some primates develop complex same-sex social grooming networks, while birds primarily allopreen reproductive mates), the social functions of social grooming are highly similar in various species (de Waal, 1997; Fraser & Bugnyar, 2012; Pitter & Christiansen, 1997; Radford & Du Plessis, 2006; Seyfarth, 1977; Silk et al., 2006; Spoon, 2006; Watts, 2000; Wilkinson, 1986). Among male chimpanzees, for instance, allogrooming is one of the primary mechanisms through which familiarity is developed and the willingness to form alliances and cooperate in the protection of territory and resources is established (Watts, 2000). Male dolphin alliances, which are commonly compared to chimpanzee alliances, appear to use physical touch similarly; individuals use their pectoral fins to stroke each other as part of partnership formation (Connor, 2007). Among birds, allopreening is fundamental to courtship, playing a substantial role in the establishment of a reproductive relationship. Like chimpanzee and dolphin alliances, avian reproductive pairs form cooperative partnerships that involve joint actions directed at resource defence (in addition to the cooperation of

rearing offspring; Forshaw, 2006; McLean, Smith, & Stewart, 1986; Renton, 2004; Welbergen & Davies, 2009).

Social grooming has also been found to play a significant role in the prevention or reduction of aggression. Monkeys, for instance, have been observed to de-escalate agonistic encounters by initiating grooming (Schino, Scucchi, Maestriperi, & Turillazzi, 1988). In the common guillemot, a cliff-nesting bird, a negative correlation was found between frequency of agonistic encounters and allopreening rate between breeding neighbours; this relationship appears to have important fitness implications, as neighbours with high rates of aggression demonstrated lower breeding success (Lewis et al., 2007). Social rank has also been found to be associated with social grooming behaviour, particularly in primates (Cheney, 1992; Schino, 2007). Seyfarth (1977), for example, found a significant correlation between dominance hierarchies and grooming distribution among social networks of female monkeys. Although avian social structures do not appear to be characterized by the presence of clear dominance hierarchies like those observed in many primates, variations in allopreening equity and aggressive encounters between affiliated individuals suggest the presence of social rank dynamics. Dominant green and red-billed woodhoopoes (cooperative breeders), for example, were found to receive significantly higher rates of body allopreening than subordinates; allopreening that was focused on the head and neck, however, was found to be consistent across roost members. The researchers argued that, as birds cannot self-groom the head/neck, allopreening that is focused on this body region has a hygienic function, while allopreening that is focused on the rest of the body serves a social function and is related to the establishment of rank (Radford & Du Plessis, 2006). These findings were consistent with findings from an earlier study on jackdaws (Katzir, 1983). Among psittacine species, variation has been found in the number of

grooming partners individuals have, amount of grooming that is done by males versus females, proportion of time dedicated to grooming different body regions, and strength of associations between allopreening and agonistic encounters between partners (Forshaw, 2006; Seibert, 2006; Spoon, 2006; Spoon, Millam, & Owings, 2007). It can therefore be concluded that allogrooming/allopreening measures are vital to the study of relationship quality across a wide variety of social species.

The degree to which individuals demonstrate synchrony or coordination in their behaviours, also provides a means through which an affiliative relationship can be measured. As indicated in the above discussion, avian pair bonds, and primate and dolphin alliances, engage in various joint actions for mutual benefit. Being able to simultaneously produce the same behaviour as, or exhibit behaviour that is complementary to, that which is expressed by a partner is argued to be fundamental to whether pair bonds or alliances can cooperate to achieve common goals (Dunbar & Shultz, 2010; Emery, Seed, et al., 2007). Among avian species that practice bi-parental care, reproductive success is highly dependent upon the coordination and/or synchrony of behaviour by mates. Evidence of this was provided by a study of captive cockatiels (a small parrot species). Researchers used proximity, allopreening, agonistic, and synchrony measures to define behavioural compatibility between mates; they found that mates with higher compatibility scores demonstrated better coordination of egg incubation behaviour, and as a result, they produced more fledglings than less compatible pairs (Spoon et al., 2006). For birds that produce altricial young, which experience long periods of dependency, the capacity to coordinate behaviour over a prolonged period is particularly important. Parrots, for instance, must inhabit nest sites for several months; their ability to synchronize and/or coordinate behaviour to protect nest sites from predators or competitors is critical to reproductive success (Forshaw,

2006; Renton, 2004; Renton & Salinas-Melgoza, 1999). This behaviour, as noted earlier, is similar to the coordination demonstrated by primate and dolphin alliances in the protection and acquisition of resources (Boehm, 1997; Byrne & Whiten, 1997; Connor & Micklethwaite-Peterson, 1994; Möller et al., 2001).

Synchronized and/or coordinated vocalizations provide additional mechanisms through which avian social bonds are maintained and expressed. Duetting, for instance, has been observed in a range of birds, often during courtship, and is believed to serve several social functions. These vocal interactions are generally characterized by the coordination of vocal patterns, and have been argued to signal commitment to a partner (preventing the loss of that partner to a competitor) and/or the presence of a collaborative partnership willing to defend resources (Arrowood, 1988; Hall, 2004; Wickler & Seibt, 1980). It has also been noted that among some parrots, such as macaws, vocalizations appear to have a mimetic value – when one partner begins to vocalize, the other almost immediately engages in the same type of vocalization (Forshaw, 2006; Radford & Du Plessis, 2006). The use of vocalizations to strengthen bonds or as social displays is not unique to birds. Positive correlations have been found, for instance, between relationship quality measures (e.g., allogrooming, proximity, or relationship stability) and intensity, frequency, and/or durations of vocal interactions among primates (e.g., pant hoot chorusing among male chimpanzees, Fedurek, Machanda, Schel, & Slocombe, 2013; duetting in gibbon pair bonds, Geissmann & Orgeldinger, 2000).

Some birds also demonstrate synchronous body movements during courtship or social displays; examples include the parallel rushing display seen in western grebes ('running' across the surface of the water in erect postures), and the synchronized bowing and tail-fanning seen in rooks (Nuechterlein & Storer, 1982; Seed, Clayton, &

Emery, 2007). Body movement synchrony such as this appears to be less common among mammals. The synchrony displayed by bottlenose dolphins provides the strongest example of body movement synchrony in a mammalian species; it is a consistent feature of mother-calf and male alliance relationships (Fellner, Bauer, & Harley, 2006). As previously indicated, researchers have argued that the ability to synchronize or coordinate with a partner is highly significant, as it suggests that an individual is 'in tune' with their partner - able to read and respond to their partner's social cues (Emery, Seed et al., 2007).

Willingness to come to the aid of an individual that is engaged in an agonistic encounter with another group member is also considered a strong indicator of a highly valued affiliative relationship (Emery, Seed et al., 2007; Fraser & Bugnyar, 2010, 2012; Nishida, 1983; Watts, 2002). Due to the potential cost of becoming involved in an aggressive interaction, an individual's willingness to provide agonistic support to a social partner is demonstrative of the extent to which they are invested in the relationship and are motivated to strengthen it. Like primates, dolphins, and several species of social carnivores, birds have been found to provide agonistic support to affiliative partners (Connor, 2007; Emery, Seed et al., 2007; Fraser & Bugnyar, 2010, 2012; Nishida, 1983; Smith, Van Horn, Powning, Cole, Graham, Memenis, & Holekamp, 2010; Watts, 2002). This behaviour has been observed in various psittacine species (Renton, 2004; Siebert, 2006, Spoon, 2006). Yellow-naped Amazons, for example, engage in coordinated chases and duets when one or both partners is/are threatened (Wright & Dorin, 2001). Among corvids, evidence of 're-directed aggression' has been reported. This occurs when, after an agonistic interaction with one individual, members of an alliance will jointly re-direct their aggression towards

the partner of the one who aggressed against them (Emery, Seed et al., 2007; van Horik et al., 2012).

Food sharing, which may include courtship feeding, the transfer of a monopolisable food item, or access to monopolizable food, is found among many species and is also recognized as an indicator of relationship quality (de Kort, Emery, & Clayton, 2006; de Waal, 1997; Porter, Moore, & White, 1981; Scheid, Schmidt, & Noë, 2008; Wolovich, Perea-Rodriguez, & Fernandez-Duque, 2008). Among birds, food sharing primarily occurs in the form of allofeeding, which is when one individual regurgitates into the mouth of another (Seibert, 2006). Allofeeding allows for the provisioning of food to young, as well as mates during egg incubation. This behaviour, however, also occurs outside of the breeding context, and is commonly observed among socially monogamous birds. Referred to as courtship feeding, this type of food sharing is believed to contribute to the formation and maintenance of avian pair bonds (Smith, 1980; Spoon, 2006). Psittacine species show a great deal of variation in the extent to which they exhibit courtship feeding. It is most commonly found among species in which only the female incubates eggs (Spoon, 2006). Furthermore, for some psittacines, courtship feeding appears to be restricted to copulation contexts (eg., Puerto Rican Amazons; Snyder, Wiley, & Kepler, 1987), usually occurring shortly before or shortly after copulation. Other species, however, demonstrate courtship feeding over prolonged periods, and in some cases, outside the breeding season; this has been seen, for example, in white-fronted Amazons, red-fronted macaws, and several conure and lovebird species (Garnetzke-Stollmann & Franck, 1991; Pitter & Christiansen, 1997; Skeate, 1984). Additionally, while it is most common to find that males allofeed females, some species also show allofeeding from females to males (Pitter & Christiansen, 1997; Seibert, 2006; Spoon, 2006).

Food transference (placing a food item directly into a partner's beak), although believed to be much less common among birds than courtship feeding, has been documented in controlled corvid studies and appears to serve important social functions in some species (de Kort et al., 2006; Scheid et al., 2008). Among rooks, food transference (also referred to as food offering) was primarily observed in higher ranking males, suggesting it may serve as a signal of individual fitness (Scheid et al., 2008). In contrast, a study on jackdaws found no such relationship, but instead reports that food offering appeared to be best explained by harassment avoidance (avoidance of begging by group members) and reciprocity; food offering between individuals was positively correlated (each partner offering food to the other), as was allopreening and food offering (de Kort et al., 2006). It should also be noted that receiving allopreening from a social partner and the degree of agonistic support offered to that partner have also been found to be correlated in some corvid species, providing further evidence of reciprocity in corvid relationships (Fraser & Bugnyar, 2012). Reciprocal relationships such as these are also found in primates and bats (de Waal, 1989, 1997; Schino, 2007; Wilkinson, 1984; 1986).

Indicators of social tolerance. Social tolerance, which refers to the degree to which one individual tolerates another, is an additional dimension of relationship quality that has also undergone investigation (Ciani, Dall'Olio, Stanyon, & Palagi, 2012; Seed, Clayton, & Emery, 2008; Van Schaik, Fragaszy, & Perry, 2003). While courtship feeding and food offering provide examples of behaviours individuals engage in in order to establish or maintain relationships, co-feeding (feeding from the same monopolizable food source) is considered to be an indicator of social tolerance rather than a reflection of an individual's active investment in a relationship (Seed et al., 2008; Rohwe & Ewald, 1981). Rohwer and Ewald (1981), for instance, found

significant differences between co-feeding rates among Harris' sparrows that were correlated with social rank; they found that dominant birds showed less tolerance of subordinates than of other dominants, displacing subordinates more frequently from shared food sources. Among rooks, Scheid and colleagues (2008) found that co-feeding primarily occurred between pair bonds. Similarly, co-feeding among primates has been found to occur most often when individuals are related; degree of familiarity and presence of a grooming relationship, however, also appear to be important factors in its occurrence (Belisle & Chapais, 2001; King, Clark, & Cowlshaw, 2011; McGrew, 1975; Pastor-Nieto, 2001).

In addition to measuring affiliative behaviours, investigations of partnership quality very often involve analyses of agonistic interactions. This is the most commonly used approach to assessing social tolerance (Bernstein, 1976; de Waal, 1986; Fraser & Bugnyar, 2010; Melis, Hare, & Tomasello, 2006; Spoon et al., 2006, 2007). Psittacine and corvid researchers, for instance, have used frequency of aggressive encounters in their social tolerance measures, which were used to assess compatibility among bonded individuals (Fraser & Bugnyar, 2010; Spoon et al., 2006). As previously indicated, Spoon and colleagues found a significant relationship between cockatiel pair bond compatibility and reproductive success. Fraser and Bugnyar found that compatibility among ravens was associated with relatedness, with birds showing greater tolerance to kin than non-kin; compatibility was also associated with sex, with tolerance being lowest in female-female relationships (Fraser & Bugnyar, 2010). Similarly, Seibert and Crowell-Davis (2001) found sex-related differences in social tolerance exhibited by cockatiels, with males exhibiting significantly more aggressive behaviours towards flock members than females. Researchers have also shown that agonistic encounters between cockatiel mates occur significantly less frequently than

between non-mates (Spoon, 2006). Among wild red-fronted macaws, the opposite was found, with bonded pairs engaging in more agonistic interactions than non-affiliated individuals (Pitter & Christiansen, 1997). The authors explain, however, that they observed very little social interaction (of any kind) among non-affiliated individuals. They further note that field studies are likely to yield different results with regards to frequency of aggressive encounters than captive studies, as captive flock members are far more likely to interact with non-mates than wild birds. Using agonistic measures as a means of assessing social tolerance can be additionally found in primate and dolphin research (Bernstein, 1976; de Waal, 1986; Samuels & Gifford, 1997; Scott, Mann, Watson-Capps, Sargeant, & Connor, 2005). Among birds, negative correlations have been found between dyadic affiliative interactions (e.g., allopreening) and agonistic interactions (Emery, Seed et al., 2007; Spoon et al., 2006).

As the above discussion illustrates, there is a wealth of information that can be gathered by observing and analysing stable relationships in socially complex animals, such as psittacines. The observational study I conducted and present here is, to my knowledge, the first comprehensive assessment of relationship quality in OWAs and BGMs. These species are known to be ‘typical’ parrots, forming and maintaining pair bonds throughout their lives (see Chapter 3), and are therefore ideal subjects for relationship quality research.

Observational study overview. The present observational study investigates relationship quality in captive OWAs and BGMs. Each species was flock-housed, allowing individuals to self-select social partners. As Spoon (2006, p.63) notes, observations on flock-housed parrots provide more “valid and reliable scientific information” than observations conducted on pair-housed individuals because semi-natural environments allow for the expression of behavioural variation. I used social

behaviour, proximity, and time budget measures, based on previous avian research, to identify focal individuals' preferred social partners and to assess the nature of those relationships. The primary objectives of this study were to contribute to our understanding of relationship quality in psittacine pair bonds, and to develop a measure of pair bond strength that could be used to investigate the potential association between relationship quality and cognitive complexity (see Chapters 5 and 7). My specific research aims included the following: (1) to identify types of affiliative interactions OWAs and BGMs engaged in (2) to create composite indices comprised of affiliative behaviours, providing a measure of energy invested by focal birds in maintaining social relationships (3) to use composite affiliative indices to identify each focal bird's preferred social partner (4) to examine relationship quality in those dyads more closely, by assessing the degree of social tolerance focal birds showed towards their preferred social partners, and assessing the quality of their allopreening relationship (including examining mutual allopreening and body regions most frequently allopreened) (5) to assess within group and between group variation in relationship quality between focal birds and their preferred social partners.

Methods

Research Site. Research was conducted at Lincolnshire Wildlife Park, a parrot sanctuary and licensed zoo. The zoo houses the largest collection of re-homed parrots in the United Kingdom, consisting of approximately 1,700 birds, representing over 100 species. All of the parrots at the zoo were voluntarily surrendered by owners who were unable to continue to care for them.

Selection of a BGM sample. As all BGMs kept at Lincolnshire Wildlife Park were housed together in one large macaw enclosure, which contained over 100

individuals and included other species, it was necessary to select a sample from that aviary for this study. Random sampling could not be used, as it was necessary to ensure that established pairs would not be separated. Subjects were instead selected in a semi-random manner, which consisted of the following: I offered peanuts to birds in the macaw enclosure. BGMs that obtained peanuts were marked using non-toxic nail polish (on one toe nail; nail polish colour and/or nail marked varied per individual). Marked individuals were observed for approximately 15 min three to four times a day for four days. BGMs that were seen in close proximity to, and/or engaging in allopreening with marked individuals on three or more consecutive occasions were also marked (if they were not already marked). Their identification information and the identity of the BGM they appeared to have an affiliative relationship with were recorded. All marked individuals (nine BGMs) were observed over another four day period following the same procedure as before. No new affiliative partners were identified during the second observational period. Marked BGMs, which consisted of four affiliated pairs and one single BGM that was not seen in close proximity to the same individual more than once and was never observed allopreening, were then moved (by zoo staff) to another aviary.

In addition to the nine birds obtained from the large aviary, three BGMs that had recently arrived at the zoo and had been in quarantine (as was part of the zoo's normal parrot in-take procedure), also joined the BGM study group. Two of the birds, which had been surrendered by different owners and therefore had no prior relationship, were housed together in quarantine and had reportedly developed an affiliative relationship, often seen allopreening by zoo staff. The other BGM had been transferred from another zoo and had been housed by itself for approximately a year at that zoo (after the death of its partner). Two single birds were included in the study

group to provide paired individuals with the opportunity to interact with unpaired birds. It was believed that this would allow for a range of affiliative investment to be expressed among BGMs. Furthermore, the uneven number of OWAs suggested that there was at least one unpaired bird in that group; thus, including single BGMs made the BGM group more comparable to the OWA group.

OWA sample. The OWA enclosure at Lincolnshire Wildlife Park housed a much smaller number of birds ($N = 23$) as compared to the macaw enclosure, and did not contain other species. As such, it was not necessary to follow the sample selection procedure as was used with the BGMs with the OWAs; observations were completed on birds that were part of this established flock. **Subjects.** OWAs ($N = 14$, nine males, five females) and BGMs ($N = 11$, seven males, four females) that participated in cognitive testing were the focus of this observational study (flock mates that did not participate in cognitive testing were excluded from this study). All subjects were believed to be adults, though their exact ages were unknown. Study groups consisted of non-breeding birds.

Identification. Prior to data collection commencing, all OWAs were ringed with coloured leg rings and were assigned corresponding leg ring ID codes that were unique in their groups (including flock members that were not study subjects). BGMs were identified using several methods, including unique physical traits (e.g., missing toe nails, face line patterns, length of beak), and presence or absence of a leg ring (half had leg rings that were engraved with unique codes). Additionally, to ensure that BGMs could be identified from a distance, individuals were marked on different body regions with different coloured food dyes.

Housing and diet. Each species was flock-housed in its own outdoor aviary (OWAs = 5.5 x 2.4 x 2.3 m; BGMs = 7.2 x 4.7 x 2.6m). Focal birds were housed with

individuals (OWA, $N = 9$; BGM, $N = 1$) that were not study subjects (birds that did not participate in cognitive testing). Enclosures contained covered areas that provided shelter from wind and rain and could be freely accessed by birds. Aviaries contained natural wood perching throughout. Subjects' diets consisted of approximately 70% fresh fruit and 30% seed. Feeding occurred twice a day (seed in the morning and fruit in the afternoon). Water was provided ad libitum.

Data collection period. OWA observations were conducted between April and September, 2012. BGM observations were conducted between May and September, 2013.

Materials. A Panasonic SDRH40 video camera mounted on a tripod was used, as well as a digital stop watch, a clipboard, and datasheets.

Procedure.

Habituation. BGMs were given two weeks to habituate to their new enclosure prior to the commencement of observations. For both species, habituation to a camera took place during the week prior to observations commencing; the camera was set up in front of the enclosures twice a day (mornings and afternoons) for 30 min.

Sampling. Observational sessions were conducted in the mornings, between 7:30 and 9:30 am, and in the afternoons, between 4:30 and 6:30 pm. Focal sampling was employed (Altmann, 1974), and each focal sample lasted 30 min. Each subject had eight focal samples, four in the morning and four in the afternoon. Observations were spread out throughout the data collection period for all subjects.

During the 30 min period, the focal individual was filmed and all behaviours of interest were verbally commentated. As a measure of association, instantaneous scan sampling (every 2 min throughout sample period) was used to identify a focal bird's nearest neighbour and their proximity to that individual (see Table 4.1). All-occurrence

sampling (Altmann, 1974) was used to record all focal bird social interactions, both affiliative and agonistic (see Table 4.1). The focal bird's social partner during these interactions (who the interactions were with) was also recorded.

Video coding. Videotaped observational sessions were coded using The Observer XT 10 program. The coding scheme used can be seen in Table 4.1. Allopreening was coded as individual interactions and as bouts (comprised of allopreening interactions). In cases in which there was mutual grooming, the area being groomed on the focal bird was coded. During coding, it was found that dyads would often switch from synchrony to coordination, and vice versa, within the same bout. Because these behaviours were often intertwined, the decision was made to collapse the categories. When dyads switched from one behaviour to the other during a single bout (see Table 4.1), only the behaviour the dyad was engaging in at the start of the bout was recorded.

Table 4.1

Coding Scheme Used to Identify Behaviours of Interest within the Videotaped Focal Observations

Behavioural category	Definition
Neighbour proximity	The physical proximity between the focal bird and its nearest neighbour is coded (contact = dyad is in physical contact; within reach = focal is within 15 cm of neighbour; far apart = focal is further than 15 cm from neighbour). The neighbour's identity is recorded.
Allopreening interaction	The focal bird is preening, and/or is being preened by, another individual. The focal bird's role is coded (donor = focal is preening partner; receives = focal is being preened by partner; mutual = focal bird and partner are simultaneously preening each other). The region of the body being groomed is coded (head = head and neck, up to the shoulders; vent = cloaca; body = all regions except head/neck and vent). The partner's identity is recorded.
Allopreening bout	Individual allopreening interactions are coded as a bout if they occur within 5s of each other.
Synchrony	The focal bird and its nearest neighbour are moving their bodies in the same manner in unison, are vocalizing in the same manner in unison, or are flying, climbing or walking in unison. The neighbour's identity is recorded. A bout ends when the last synchronized movement or vocalization ends and no other synchronous behaviour occurs for at least 3 s.
Coordination	The focal bird and its nearest neighbour are moving their bodies or vocalizing in the same manner, in an alternating fashion. The neighbour's identity is recorded. A bout ends when the last coordinated movement or vocalization ends and no other coordinated behaviour occurs for at least 3 s.
Agonistic support	The focal bird is involved in third party intervention in an agonistic interaction (an individual not initially involved in an agonistic interaction comes to the aid of one of the birds, directing aggression towards that individual's opponent). The focal bird's role is coded (receives support or gives support). The identity of the individual the focal bird supports or who comes to the aid of the focal is coded.
Courtship feeding	The focal bird is engaged in allofeeding – one parrot grasps another's beak and regurgitates into their mouth. The identity of the focal bird's partner is recorded.
Co-feeding	The focal bird is feeding from the same food dish as another individual and they are within reach or in contact. The feeding neighbour's identity is recorded.
Agonistic	The focal bird directs aggression at another individual. Agonistic behaviours include pecking, squawking, displacement (forced physical retreat), kicking or defensive foot (raising a foot at another bird). The victim's identity is recorded.
Approach tolerance	The focal bird is approached by another individual (coming within 15 cm of the focal bird). The focal bird's response is coded (neutral = no response; agonistic = directs aggression towards the individual; affiliative = engages in allopreening with the individual within 5 s of the approach). The approaching individual's identity is recorded.
Pilfer tolerance	The focal bird is holding a food item and another parrot takes it or attempts to take it. The focal bird's response is coded (tolerates = no agonistic behaviour is directed at pilferer; agonistic response = focal bird directs agonistic behaviour(s) at pilferer).
Time budget	The type of behaviour the focal bird is engaging in is coded (maintenance = autopreening, scratching, or bill wiping; ingestive = eating or drinking;

locomotion = walking, climbing, or flying; social interaction = any social interaction; other = undefined behaviour).

Visibility The focal bird is coded as 'visible' when their behaviour can be seen, and 'not visible' when it cannot be clearly seen.

Data analysis. I used the Observer program to extract raw scores (duration and/or frequency) for behaviours listed in Table 4.1. These behaviours were used for create indices, as outlined below. Two-tailed nonparametric tests were used for within and between species analyses due to small sample sizes and/or because data were not normally distributed. Due to small sample sizes, exact rather than asymptotic p-values are reported (as recommended by Mundry & Fischer, 1998). As recommended by Field (2009), *r* values are reported as measures of effect sizes (.10 = small effect, .30 = medium effect, .50 = large effect).

Creation of behavioural indices. For each affiliative behaviour, the percentages of OWA and BGM focal birds that exhibited the behaviour at least once were calculated (including, within reach proximity, in contact proximity, allopreening bout, synchrony/coordination, courtship feeding, and agonistic support). Indices were created for all behaviours displayed by 50% or more of focal birds. Rates of behaviour between each focal (OWA, *N* = 14; BGM, *N* = 11) and all potential social partners (OWA, *N* = 22; BGM, *N* = 11) in the aviary were calculated. Rates of behaviour were calculated as a function of the opportunity to display that behaviour. Calculations were unidirectional (e.g. focal bird engaging in behaviour towards partner) for all indices to capture the energy the focal bird was investing in the relationship. The formulae used to calculate rates for each behaviour are provided below, with A representing the focal, and B representing the partner.

Close proximity. The total number of proximity scans when B was the nearest neighbour to A and was in contact or within reach, divided by A's total proximity scans:

$$\frac{A_f(B_{wr} + B_{ct})}{A_{fps}}$$

Where A_f = Bird A is the focal individual; B_{wr} = scans where Bird B is nearest neighbour within reach; B_{ct} = scans where Bird B is nearest neighbour in physical contact; A_{fps} = total number of bird A's proximity scans.

Allopreening bouts. The total frequency of A's allopreening bouts with B, divided by A's total focal visible time:

$$\frac{A_f(B_{ab})}{A_{fv}}$$

Where A_f = Bird A is the focal individual; B_{ab} = total frequency of allopreening bouts where Bird B is the allopreening partner. A_{fv} = Bird A's total focal visible time

Allopreening interactions. The total duration of A's allopreening interactions with B (including all focal roles and body regions, see Table 4.1), divided by A's total focal visible time:

$$\frac{A_f(B_{ai})}{A_{fv}}$$

Where A_f = Bird A is the focal individual; B_{ai} = total duration of allopreening interactions where Bird B is the allopreening partner; A_{fv} = Bird A's total focal visible time.

Allopreening location. For each body region (see Table 4.1), the total duration of allopreening between A and B that was focused on that body region (including all focal roles, see Table 4.1), divided by A's total duration of allopreening interactions with B:

$$\frac{A_f(B_{ai})}{A_f(B_{ai})}$$

Where A_f = Bird A is the focal individual; B_{ai} = total duration of allopreening interactions focused on the body region where Bird B is the allopreening partner; B_{ai} = total duration of all allopreening interactions where Bird B is the allopreening partner

Synchrony and coordination. The total frequency of synchronous/coordinated behaviour that occurred between A and B when A was the focal, divided by A's total focal visible time:

$$\frac{A_f(B_{sc})}{A_{fv}}$$

Where A_f = Bird A is the focal individual; B_{sc} = frequency of synchronous/coordinated behaviour when B was the nearest neighbour; A_{fv} = Bird A's total focal visible time.

Courtship feeding. The number of instances that A was engaged in courtship feeding with B, divided by A's total feeding time (estimated as the number of ingestive time budget scans, multiplied by 2 min):

$$\frac{A_f(B_{af})}{A_{ft}}$$

Where A_f = Bird A is the focal individual; B_{af} = total frequency of courtship feeding where Bird B was the feeding partner; A_{ft} = Bird A's total feeding time.

Agonistic display. The total number of agonistic behaviours A directed towards B when A was the focal, divided by A's total visible time:

$$\frac{A_f(B_{ag})}{A_{fv}}$$

Where A_f = Bird A is the focal individual; B_{ag} = total number of agonistic behaviours directed at Bird B; A_{fv} = Bird A's total focal visible time.

Approach tolerance. The total number of instances B approached A, and A demonstrated a neutral or affiliative response was divided by the total number of times B approached A:

$$\frac{A_f(B_{nr} + B_{ar})}{A_f(B_{at})}$$

Where A_f = Bird A is the focal individual; B_{nr} = total number of neutral responses when Bird B approached; B_{ar} = total number of affiliative responses when Bird B approached; B_{at} = total number of approaches by Bird B.

Within species analyses.

Creation of composite social partner scores. Individual affiliative behaviours were combined in order to create composite social partner scores. This allowed for the identification of focal birds' 'preferred' social partners. Based on previous research, the following behaviours were considered for inclusion in social partner composite scores: close physical proximity, allopreening interaction, coordination/synchrony, courtship feeding, and agonistic support; these behaviours were identified as indicators of focal investment in social relationships. However, individual behaviour indices were excluded from composite indices if less than 50% of focal birds (within species) did not have scores for those categories. Close proximity, allopreening duration, and synchrony/coordination were included in OWA and BGM composite indices. BGM indices also included courtship feeding.

Composite social partner scores were created by (i) standardizing (within species) individual affiliative behaviour indices (e.g. for close proximity, calculating a mean and standard deviation of proximity scores across all possible dyads (OWAs, $N = 308$; BGMs, $N = 121$) so these could be used to calculate a proximity z-score for each dyad) and (ii) summing the standardized behavioural indices (OWAs, $N = 3$; BGMs, $N = 4$) for each dyad. For each focal bird (OWAs, $N = 14$; BGMs, $N = 11$), a mean and

standard deviation were calculated from their composite affiliative scores with all possible partners (OWAs, $N = 22$; BGMs, $N = 11$). Any social partner with whom the focal individual had a score that was higher than 1SD above their mean was classified as an affiliative partner for the focal bird. The affiliative partner with whom the focal bird had the highest score was identified as the preferred social partner.

Focal bird-preferred partner analyses.

Creation of composite preferred partner affiliation index and preferred partner social tolerance index. Composite preferred partner affiliation scores were created in order to assess within species variation in affiliative investment by focal birds in their relationships with preferred partners. In line with the social partner composite scores outlined above, composite preferred partner affiliation scores were based on proximity, allopreening duration and synchrony/coordination scores for OWA, plus courtship feeding for BGMs. However, for the composite preferred partner affiliation scores, individual behaviour indices were calculated by standardizing scores (within species) only across focal birds and their preferred partners (OWAs, $N = 14$; BGMs, $N = 11$).

Based on previous avian research, agonistic behaviour, approach tolerance, pilfer tolerance and co-feeding were identified as social tolerance indicators and considered for inclusion in social tolerance composite scores (Arrowood, 1988; de Kort et al., 2006; Fraser & Bugnyar, 2010; Seed et al., 2008; Spoon et al., 2006). However, co-feeding and pilfer tolerance were excluded because they rarely occurred - three OWAs had scores in each of these categories and only one BGM had a score for co-feeding; none of the BGMs had scores for pilfer tolerance. Agonistic display and approach tolerance indices were standardized within species. Dyads that did not have scores for approach tolerance (OWA, $N = 2$; BGM, $N = 1$), where preferred partners were never observed approaching the focal bird, were excluded from this analysis. For

each preferred partner dyad with scores in both behavioural indices (OWAs, $N = 12$; BGMs, $N = 10$), standardised agonistic display scores were subtracted from the standardised approach tolerance scores in order to create a composite social tolerance index, referred to as ‘composite preferred partner tolerance index.’

Correlational analyses of composite preferred partner affiliation index and composite preferred partner tolerance index. Kendall’s tau tests examined the relationships between affiliation indices and composite preferred partner tolerance indices to test the hypothesis that focal bird investment in relationship maintenance was positively correlated with the tolerance they demonstrated towards their preferred partners. Dyads without a composite preferred partner tolerance score were excluded from this analysis, meaning 12 OWAs and 10 BGM contributed to their respective analyses.

Social tolerance exhibited by focal birds towards preferred partners and other partners. In order to determine whether focal birds would show greater tolerance of partners compared to non partners the following were compared using two-tailed Wilcoxon signed rank tests: (1) proportions of total agonistic displays focal birds directed towards partners and non-partners (2) proportions of total approaches focal birds tolerated from partners and non-partners.

Allopreening. Two-tailed Wilcoxon signed rank tests were run to (1) determine whether the proportion of time focal birds and preferred partners spent engaged in head allopreening was significantly higher than the proportion of time they spent engaged in body or vent allopreening (2) compare proportion of time focal birds engaged in allopreening with preferred partners that was mutual as compared to unidirectional. Kendall’s tau tests were run to determine whether the proportion of time focal birds and

preferred partners spent engaged in mutual allopreening was significantly correlated with composite preferred partner affiliation scores.

Between species analyses.

Individual behavioural indices. Behavioural indices for focal-preferred partner interactions were standardized across all birds (both species, $N = 25$) for between species analyses. Individual affiliative indices (close proximity, allopreening interactions, synchrony/coordination, and courtship feeding) and individual social tolerance indices (agonistic display and approach tolerance) were compared between OWA and BGM preferred partner dyads, using Mann Whitney U tests.

Composite affiliative investment scores. When considering all focal birds, more than 50% engaged in courtship feeding, so the composite index was calculated for each bird as the sum of the standardised courtship feeding, close proximity, allopreening duration and synchrony/coordination scores. OWA and BGM composite affiliative investment scores were compared using a Mann Whitney test.

Composite social tolerance scores. Agonistic display and approach tolerance indices were standardized across species for focal birds (agonistic display, $N = 25$; approach tolerance, $N = 22$) and preferred partners. Agonistic display scores were subtracted from approach tolerance scores to create composite social tolerance scores, which were compared between species. Three dyads (OWAs, $N = 2$; BGMs, $N = 1$) that had no approach tolerance scores were excluded from this analysis (as well as the analysis of individual approach tolerance indices).

Allopreening. Allopreening location indices were standardized across species for between species analyses. Mann Whitney tests were run to determine whether OWA and BGM focal and preferred partners would show significant differences in (1)

proportion of time birds allopreened different body regions (head, body, or vent) (2)
 proportion of time birds engaged in mutual allopreening.

Results

Indicators of affiliative relationships.

OWAs. Being in close physical proximity with closest neighbours, allopreening, and synchrony/coordination, were exhibited by most or all OWA focal birds (see Table 4.2). Two OWAs exhibited agonistic support (observed a total of three times). No focal bird was observed engaging in courtship feeding.

BGMs. All affiliative behaviours of interest were observed in BGMs (see Table 4.2). Agonistic support was exhibited by two focal birds (displayed once by each individual).

Table 4.2

Percentage of OWA (N = 14) and BGM (N = 11) Focal Individuals that Exhibited each Type of Affiliative Behaviour

Behavioural category	Behaviour	Percentage of focal birds	
		OWA	BGM
Physical proximity	Within reach	100	100
	Contact	100	90.91
Social behaviour	Allopreening bout	100	90.91
	Synchrony/coordination	78.57	72.72
	Courtship feeding	0.00	54.55
	Agonistic support	14.29	18.18

Identification of preferred partners.

OWAs. Of 22 potential social partners, OWA focal birds had positive composite social partner scores with one to four individuals, and had one to two affiliative partners (see Table 4.3). OWA composite social partner scores were highly varied, ranging from 3.39 to 22.69; dyads consisted of opposite-sex and male-male individuals (see Table 4.4). From the 14 focal birds, 10 had reciprocal preferred

partners (e.g. Bird A's preferred partner was bird B and B's preferred partner was A), three had non-reciprocal preferred partners (e.g. Bird A's preferred partner was bird B and B's preferred partner was Bird C) and for one bird this could not be determined, as their partner was not a focal individual, so their unidirectional behavioural rates were not calculated. There were therefore a total of nine unique OWA preferred partner dyads involving focal birds.

Table 4.3

OWA Focal Birds and Partners with Positive Scores

Focal bird	Number of social partners with positive scores	Range of positive scores	Focal mean	Cut off point for being an affiliative partner (mean + 1SD)	Number of affiliative partners
Tulip	2	0.22 - 5.95	-0.28	1.13	1
Benny	1	17.55 - 17.55	0.18	4.06	1
Oliver	3	0.29 - 22.69	0.72	5.73	1
Ricky	1	1.59 - 1.59	-0.45	0.04	1
Freckles	1	9.09 - 9.09	-0.19	1.89	1
Joon	3	0.09 - 12.08	0.07	2.77	1
Belle	2	0.42 - 20.34	0.45	4.91	1
Piglet	1	13.31 - 13.31	-0.01	2.97	1
Simon	4	0.35 - 3.73	-0.19	0.77	1
Rocky	4	0.42 - 3.39	-0.20	0.79	2
Bo	4	0.58 - 4.72	-0.17	1.01	2
Pete	2	0.53 - 12.08	0.01	2.72	1
Stumpy	4	0.42 - 10.15	0.25	2.77	2
Penny	2	2.98 - 7.07	-0.14	1.65	2

Table 4.4

Composite Social Partner Scores for each OWA Focal Bird

Focal bird	Focal sex	Preferred partner	Preferred partner sex	Composite social partner score
Tulip	F	Stumpy	M	5.95
Benny	M	Joon	F	17.55
Oliver	M	Lucy	F	22.69
Ricky	M	Oliver	M	1.59
Freckles	M	Piglet	F	9.09
Joon	F	Benny	M	12.08
Belle	F	Pete	M	20.34
Piglet	F	Freckles	M	13.31
Simon	M	Penny	F	3.73
Rocky	M	Bo	M	3.39
Bo	M	Rocky	M	4.72
Pete	M	Belle	F	12.08
Stumpy	M	Bo	M	10.15
Penny	F	Simon	M	7.07

BGMs. All BGM focal birds had positive composite social partner scores with just one individual (of 11 potential social partners), with the exception of Lola, who did not have positive scores with any flock member. As such, all BGM focal birds had just one affiliative/preferred partner (see Table 4.5). Composite social partner scores were highly varied, ranging from -0.76 to 20.75; dyads consisted of opposite-sex and male-male individuals (see Table 4.6). From the 11 focal birds, eight had reciprocal preferred partners. This could not be determined for three birds; these birds had the same preferred partner, who was not a focal individual. As such, their unidirectional behavioural rates were not calculated. There were therefore a total of seven unique BGM preferred partner dyads involving focal birds.

Table 4.5

BGM Focal Birds and Partners with Positive Scores

Focal bird	Number of social partners with positive scores	Focal mean	Cut off point for being an affiliative partner (mean + 1SD)	Number of affiliative partners
Archie	1	-0.38	1.25	1
Digbee	1	0.34	4.12	1
Elvis	1	-0.33	1.45	1
Gizmo	1	0.61	5.50	1
Gwen	1	-0.46	0.80	1
Lola	0	-0.86	-0.82	1
Mouse	1	-0.69	-0.20	1
Oscar	1	1.03	7.32	1
Psycho	1	-0.29	1.62	1
Red	1	-0.11	2.41	1
Sid	1	1.15	7.65	1

Table 4.6

Composite Social Partner Scores for each BGM Focal Bird

Focal bird	Focal sex	Preferred partner	Preferred partner sex	Composite social partner score
Archie	M	Gwen	F	4.52
Digbee	M	Oscar	M	11.72
Elvis	M	Frankie	M	5.04
Gizmo	M	Sid	M	15.37
Gwen	F	Archie	M	3.32
Lola	F	Frankie	M	-0.76
Mouse	F	Frankie	M	0.76
Oscar	M	Digbee	M	19.99
Psycho	F	Red	M	5.46
Red	M	Psycho	F	7.50
Sid	M	Gizmo	M	20.75

Within species dyad analyses.***Social tolerance exhibited by focal birds towards preferred partners and other partners.***

OWAs. In both the pilfer tolerance and the co-feeding categories, only three focal birds had scores with preferred partners. As such, these categories were excluded from composite preferred partner tolerance scores. A Kendall's tau test showed that *OWA* composite preferred partner social tolerance scores (see Table 4.7) were not significantly correlated with their composite preferred partner affiliation scores, although the pattern of data showed a negative relationship between these variables ($\tau = -.28, p = .224, N = 12$).

Table 4.7. *Partner Tolerance Index Scores with Preferred Partners for each OWA Focal Bird*

Focal	Preferred partner	Agonistic display	Approach tolerance	Composite preferred partner tolerance
Tulip	Stumpy	-0.32	n/a	n/a
Benny	Joon	-0.32	0.70	1.02
Oliver	Lucy	-0.32	0.53	0.85
Ricky	Oliver	-0.32	0.70	1.02
Freckles	Piglet	0.93	0.70	-0.23
Joon	Benny	-0.32	0.26	0.58
Belle	Pete	2.75	0.70	-2.05
Piglet	Freckles	1.78	n/a	n/a
Simon	Penny	-0.32	0.33	0.65
Rocky	Bo	-0.32	0.70	1.02
Bo	Rocky	-0.32	0.70	1.02
Pete	Belle	9.63	0.70	-8.93
Stumpy	Bo	-0.32	0.70	1.02
Penny	Simon	0.81	0.26	-0.55

Thirty-six percent of OWA focal birds ($N = 14$) were found to have directed aggression towards their partners. A Wilcoxon signed rank test showed, the proportion of agonistic behaviours focal birds directed towards preferred partners ($Mdn = .00$, $IQR = .51$) was significantly lower than the proportion of agonistic behaviours they directed towards other flock members ($Mdn = 1.00$, $IQR = .51$; $z = -2.16$, $p = .031$, $r = -.58$).

Two OWA focal birds did not have scores for approach tolerance (preferred partners were not observed approaching focal birds), leaving an N of 12 for this analysis (see Table 4.7). A Wilcoxon signed rank test showed that the proportion of approaches focal birds tolerated from preferred partners was significantly greater than the proportion of approaches they tolerated from non-partners ($Mdn = .71$, $IQR = .55$; $z = -2.51$, $p = .012$, $r = -.73$).

BGMs. Only one dyad had a co-feeding index score; none of the dyads had pilfer tolerance index scores. These categories were therefore excluded from composite preferred partner social tolerance scores. A Kendall's tau test showed that the composite preferred partner social tolerance scores (see Table 4.8) BGM focal birds

had with their partners ($N = 10$) were not significantly correlated with their composite preferred partner affiliation scores ($\tau = -.24, p = .325$), but the pattern of data indicated a negative relationship between these two measures.

Table 4.8.

Partner Tolerance Index Scores with Preferred Partners for each BGM Focal Bird.

Focal	Preferred partner	Agonistic display	Approach tolerance	Composite preferred partner tolerance
Archie	Gwen	1.23	0.82	-0.42
Digbee	Oscar	-0.40	0.28	0.67
Elvis	Frankie	2.87	0.28	-2.59
Gizmo	Sid	0.54	0.82	0.27
Gwen	Archie	2.87	0.82	-2.05
Mouse	Frankie	-0.40	-1.34	-0.94
Lola	Frankie	-0.40	n/a	n/a
Oscar	Digbee	5.36	0.82	-4.55
Psycho	Red	2.05	0.64	-1.41
Red	Psycho	6.15	0.82	-5.33

Seventy-three percent of BGM focal birds were found to have directed aggression towards their partners. A Wilcoxon signed rank test showed that the proportion of agonistic behaviours focal birds ($N = 11$) directed towards preferred partners ($Mdn = .36, IQR = .67$) was not significantly less than the proportion of agonistic behaviours they directed towards non-partners ($Mdn = .43, IQR = .48; z = -.51, p = .609, r = -.15$).

One BGM focal bird did not have approach tolerance scores with their preferred partner (see Table 4.8), and two focal birds did not have approach tolerance scores with non-partners. This resulted in eight focal birds being included in the approach tolerance analysis; a Wilcoxon signed rank test showed that the proportion of approaches focal birds tolerated from preferred partners was significantly greater than the proportion of approaches they tolerated from non-partners ($Mdn = .50, IQR = .88; z = -2.00, p = .045, r = -.71$).

Allopreening.

OWA. All OWA focal birds engaged in allopreening of the head and body with preferred partners. No instance of vent allopreening was observed. A Wilcoxon signed rank test indicated that focal bird and preferred partner dyads ($N = 13$) spent significantly higher proportions of time (measured in s) engaged in head allopreening ($Mdn = .96, IQR = .09$) than body allopreening ($Mdn = .04, IQR = .09$), $z = -3.18, p = .001, r = -.85$. A Wilcoxon signed rank test also showed that the proportion of time OWA focal bird and preferred partner dyads ($N = 13$) spent engaged in unidirectional allopreening ($Mdn = .99, IQR = .06$) was significantly higher than the proportion of time they spent engaged in mutual allopreening ($Mdn = .01, IQR = .06$), $z = -3.21, p = .001, r = -.89$. A Kendall's tau test showed that mutual allopreening scores were significantly positively correlated with composite preferred partner affiliation scores ($\tau = .66, p = .003, N = 13$; see Figure 4.1).

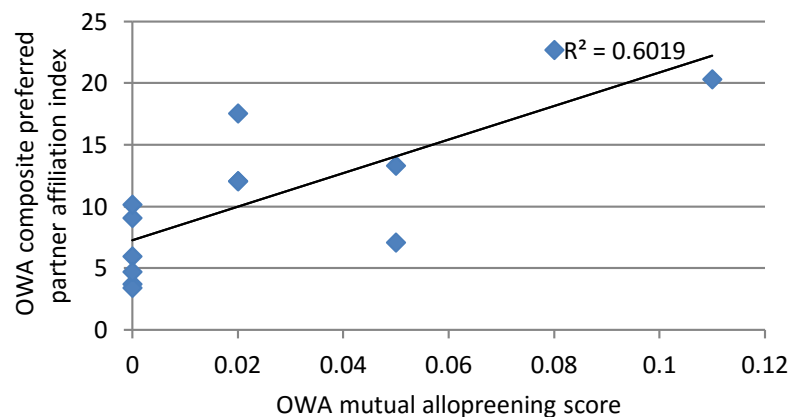


Figure 4.1. Scattergram illustrating the relationship between OWA mutual allopreening scores and composite preferred partner affiliation index scores. Line of best fit and R^2 value are illustrated.

BGMs. A Wilcoxon signed rank test showed that there was no significant difference between the proportion of time (measured in s) BGM focals and preferred partners ($N = 10$) spent engaged in head allopreening ($Mdn = .56; IQR = .29$), and the

proportion of time they spent engaged in body allopreening ($Mdn = .42$; $IQR = .25$; $z = -.97$, $p = .333$, $r = -.31$). The proportion of time focal birds and partners spent engaged in vent allopreening ($Mdn = .06$; $IQR = .08$) was significantly lower than head allopreening ($z = -2.80$, $p = .005$, $r = -.89$) and body allopreening ($z = -2.80$, $p = .005$, $r = -.89$). Wilcoxon tests also showed that the proportion of time BGM focal birds and preferred partners spent engaged in unidirectional allopreening ($Mdn = .81$, $IQR = .14$) was significantly higher than mutual allopreening ($Mdn = .20$, $IQR = .14$; $z = -2.80$, $p = .005$, $r = -.89$). A Kendall's tau test showed that mutual allopreening scores were not significantly correlated with composite preferred partner affiliation scores ($\tau = .36$, $p = .151$, $N = 10$; see Figure 4.2).

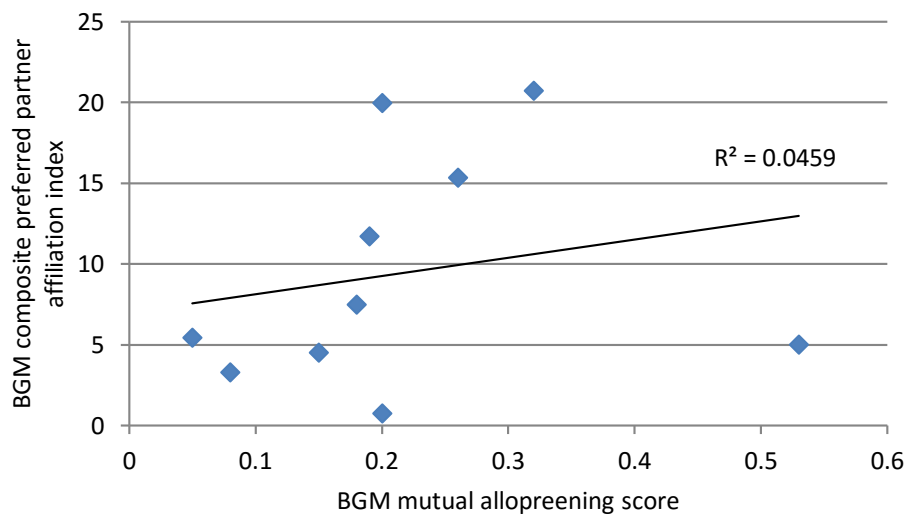


Figure 4.2. Scattergram illustrating the relationship between BGM mutual allopreening scores and composite preferred partner affiliation index scores. Line of best fit and R^2 value are illustrated.

Between species focal and preferred partner dyad analyses.

Individual behavioural indices. OWA and BGM focal bird and preferred partner dyad index scores for affiliative behaviours were compared using Mann-Whitney tests. Results indicate that while frequency of allopreening bouts was

significantly higher for OWAs, BGMs spent significantly more time engaged in allopreening interactions. BGMs also engaged in significantly more courtship feeding than OWAs. No other significant differences were found (see Table 4.9).

Table 4.9

Results from OWA and BGM Mann U Tests Comparing Standardized Scores for Individual Affiliative Behaviours for Focal Birds and their Preferred Partners

Behaviour	OWA		BGM		U	z	p	r
	Mdn	IQR	Mdn	IQR				
Proximity	-0.18	2.11	0.37	1.44	66.00	-0.60	.547	-0.12
Allopreening bout frequency	0.46	1.92	-0.70	0.22	30.50	-2.55	.011*	-0.51
Allopreening interaction	-0.45	0.36	0.19	2.93	39.50	-2.05	.040*	-0.41
Coordination/synchrony	-0.44	1.65	-0.55	0.65	65.00	-0.66	.507	-0.13
Courtship feeding			0.06	1.50	35.00	-3.07	.002*	-0.61
Gives agonistic support	-0.39	0.00	-0.39	0.00	75.00	-0.17	.864	-0.03

Mann-Whitney tests showed that there were no significant between species differences in agonistic index scores focal birds had with their preferred partners (OWA, $N = 14$, $Mdn = -.72$, $IQR = .53$; BGM, $N = 11$, $Mdn = .01$; $IQR = 1.47$ $U = 46.50$, $z = -1.77$, $p = .077$, $r = -.35$), and proportion of approaches focal birds tolerated from their preferred partners (OWA, $N = 12$, $Mdn = .46$, $IQR = .65$; BGM, $N = 10$, $Mdn = .46$, $IQR = 1.13$, $U = 51.00$, $z = -.69$, $p = .491$, $r = -.15$).

Composite affiliative investment indices. A Mann-Whitney test showed that there were no significant between species differences in the composite affiliative investment scores focal birds had with preferred partners (OWA, $N = 14$; BGM, $N = 11$; $U = 57.00$, $z = -1.10$, $p = .274$, $r = -.22$; see Table 4.10, Figure 4.3). A Mann-Whitney test showed that there were no significant sex differences (females, $Mdn = -1.48$, $IQR = 3.00$; males, $Mdn = -.26$, $IQR = 4.85$) in focal birds' composite affiliative investment scores with preferred partners (across species), $N = 25$, $U = 53.00$, $z = -1.08$, $p = .301$, $r = -.22$.

Table 4.10

OWA and BGM Unidirectional Scores with Preferred Partner in each Behavioural Category and Composite Scores

Species	Focal	Preferred partner	Proximity	Synchrony/ coordination	Courtship feeding	Allopreening interactions	Composite affiliative investment
OWA	Tulip	Stumpy	-0.07	-0.70	-0.42	-0.57	-1.76
	Benny	Joon	1.03	1.00	-0.42	0.04	1.65
	Oliver	Lucy	0.28	2.37	-0.42	0.16	2.39
	Ricky	Oliver	-1.33	-0.46	-0.42	-0.90	-3.11
	Freckles	Piglet	-0.05	-0.08	-0.42	-0.44	-0.98
	Joon	Benny	-0.28	0.60	-0.42	-0.45	-0.54
	Belle	Pete	1.11	2.26	-0.42	-0.34	2.62
	Piglet	Freckles	1.69	0.93	-0.42	-0.84	1.37
	Simon	Penny	-1.07	-0.41	-0.42	-0.79	-2.68
	Rocky	Bo	-1.27	-0.63	-0.42	-0.60	-2.92
	Bo	Rocky	-0.74	-0.70	-0.42	-0.54	-2.40
	Pete	Belle	1.16	-0.70	-0.42	-0.12	-0.08
	Stumpy	Bo	-1.05	-0.70	-0.42	-0.35	-2.51
	Penny	Simon	-0.30	-0.62	-0.42	-0.40	-1.74
Median			-0.18	-0.44		-0.45	-1.36
IQR			2.11	1.65		0.36	3.99
BGM	Archie	Gwen	0.53	-0.70	0.22	-0.73	-0.69
	Digbee	Oscar	-0.06	-0.05	2.29	0.11	2.29
	Elvis	Frankie	-0.03	-0.70	0.06	0.23	-0.44
	Gizmo	Sid	0.37	0.21	1.04	2.79	4.42
	Gwen	Archie	-0.63	-0.63	-0.42	0.19	-1.48
	Lola	Frankie	-1.92	-0.70	-0.42	-0.90	-3.93
	Mouse	Frankie	-1.38	-0.55	-0.42	-0.77	-3.12
	Oscar	Digbee	1.47	-0.26	3.74	2.20	7.14
	Psycho	Red	0.81	-0.41	-0.42	-0.24	-0.26
	Red	Psycho	1.30	-0.63	-0.42	0.92	1.17
	Sid	Gizmo	0.43	2.25	0.58	2.34	5.60
Median			0.37	-0.55	0.06	0.19	-0.26
IQR			1.44	0.65	1.46	2.93	5.90

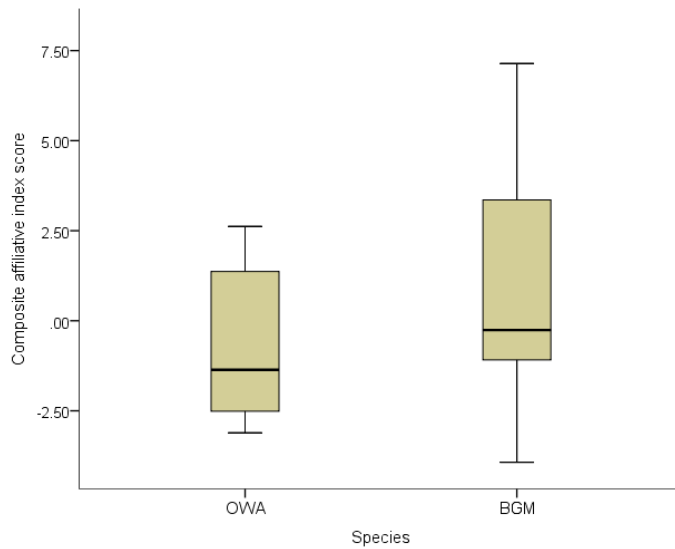


Figure 4.3. Boxplots illustrating composite affiliative investment indices for OWA ($N = 14$) and BGM ($N = 11$) dyads.

Composite social tolerance indices. Results from a Mann-Whitney test revealed that composite social tolerance scores of OWA dyads ($N = 12$) were significantly higher than BGM ($N = 10$) composite scores, $U = 24.00$, $z = -2.38$, $p = .017$, $r = -.51$ (see Figure 4.4).

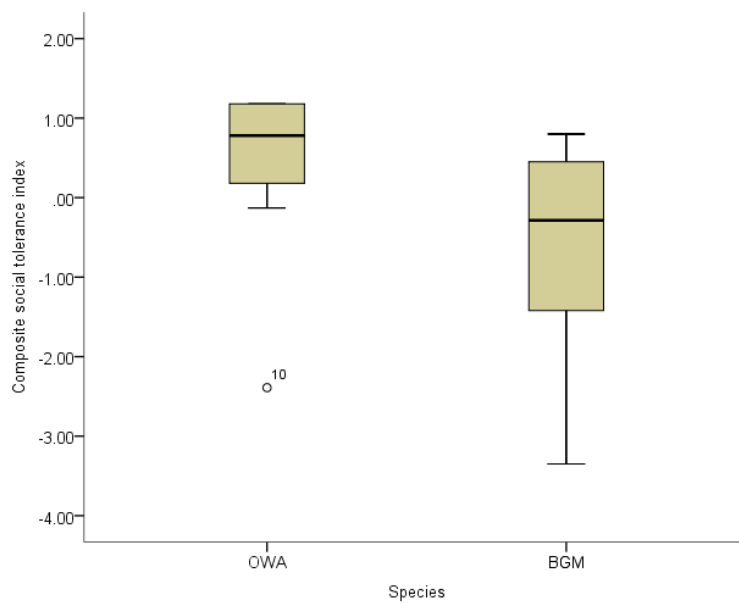


Figure 4.4. Boxplots illustrating OWA ($N = 12$) and BGM ($N = 10$) focal and preferred partner composite social tolerance indices.

Allopreening. Mann-Whitney tests revealed that OWA focal bird and preferred partner dyads ($N = 13$) spent a significantly higher proportion of time engaged in head allopreening than BGM dyads ($N = 10$; $U = 2.00$, $z = -3.82$, $p < .001$, $r = -.80$), while BGM dyads spent a significantly higher proportion of time engaged in body allopreening ($U = 4.00$, $z = -3.69$, $p < .001$, $r = -.77$) and vent allopreening ($U = 6.00$, $z = -4.00$, $p < .001$, $r = -.83$) (see Figure 4.5). Mann-Whitney tests also revealed a significant between species difference when mutual and unidirectional allopreening proportions were compared; BGMs were found to spend significantly more time engaged in mutual allopreening ($Mdn = .80$, $IQR = 1.19$) than OWAs ($Mdn = -.77$, $IQR = .41$, $U = 3.00$, $z = -3.88$, $p < .001$, $r = -.81$).

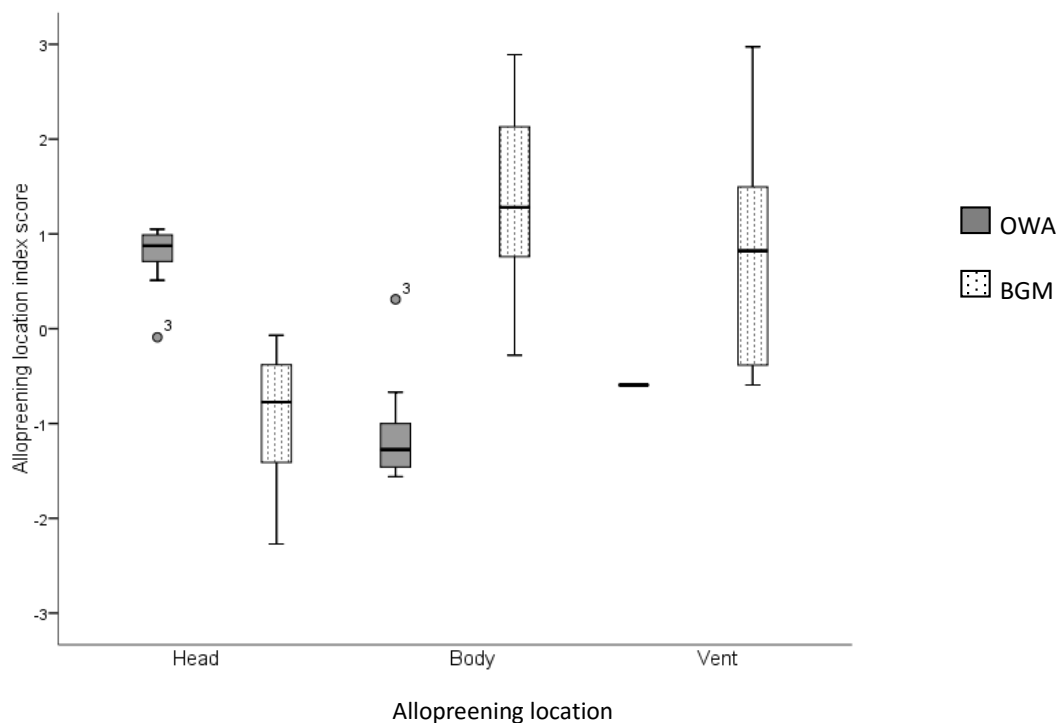


Figure 4.5. Box plots illustrating OWA and BGM focal and preferred partner index scores for head, body, and vent allopreening.

Discussion

Indicators of affiliative relationships were frequently observed in OWAs and BGMs, with both species showing evidence of pair bonding. Most or all OWA and BGM focal birds had proximity scans in which they were in contact with their nearest neighbours, and were found to engage in allopreening and synchronous/coordinated behaviour with social partners. Selective affiliative investment was observed in both groups, with birds engaging in affiliative interactions with specific individuals (preferred partners) more so than other group members, and in the majority of cases, relationships were reciprocal. Overall levels of affiliative investment were found to be similar in OWAs and BGMs, with focal birds in both species showing a high frequency (or duration) of affiliative behaviours with their preferred partners; both groups also showed a high degree of variance in composite affiliative investment scores. So although there was considerable individual variation in energy invested by individuals to maintain their pair bonds, on average, it was similar in both species. This finding supports Spoon's (2006) assertion that research conducted on flock-housed parrots is more valid than research focused on dyad-house individuals, as semi-natural conditions promote behavioural variation that is more representative species' natural social interactions.

The findings described above are consistent with descriptions of OWAs and BGMs as possessing social characteristics that are complex and typical of psittacines (Brightsmith & Bravo, 2006; Forshaw, 2006; Hoppe, 1992; see Chapter 3 for study species details). As study groups consisted of non-breeding individuals that were group-housed (and thus had access to multiple potential social partners), my research lends support to the assertion that, like corvids, psittacines selectively form bonds with

conspecifics that are actively maintained all year round (Emery, Seed et al., 2007; Shultz & Dunbar, 2010). As previously indicated, this is one of the characteristics that distinguish corvids and psittacines from other avian taxa (including other socially monogamous birds, such as geese), and importantly, has been found to be positively correlated with avian brain size (Shultz & Dunbar, 2010; see Chapter 1).

While OWAs and BGMs invested similar levels of energy in maintaining partnerships, variation was observed in some of the individual affiliative behaviours that were measured (e.g., courtship feeding and vent allopreening). These differences are important because they illustrate that although two species may show a similar propensity towards forming and maintaining strong bonds, they may differ in how these bonds are expressed. Relationship quality studies that rely on one or two behavioural categories (or define behaviours too broadly) may thus fail to identify between species variation that could be important to understanding how pair bond dynamics may be related to individual fitness, reproductive success, or cognitive variation.

Although approximately half of BGM focal birds engaged in courtship feeding, this behaviour was not observed at all in OWAs. This was unexpected, given that courtship feeding commonly occurs in psittacine species that practice female-only incubation (Spoon, 2006). However, this finding is not entirely surprising as some species that are female-only incubators appear to engage in courtship feeding primarily during breeding seasons, often shortly before or after copulation (e.g., Puerto Rican Amazons, which are closely related to OWAs, Snyder et al., 1987). It is therefore likely that it would have been observed if the OWA group had consisted of breeding pairs. Still, if this finding is representative of a species difference, and BGMs engage in courtship feeding outside the breeding context, while OWAs do not, one has to wonder why this is. This question also arises when one considers that vent

allopreening, like courtship feeding, was not observed at all in the OWA study group, but was demonstrated by approximately half of BGM focal birds and preferred partners (though it occurred significantly less than head or body allopreening). Both of these behaviours (vent allopreening and courtship feeding) are most commonly observed in mated and breeding avian pair bonds (Butler, Hazelhurst, & Butler, 2002; Schneider, Serbena, & Guedes, 2006; references for courtship feeding). Thus, these observations suggest that BGMs may rely on a greater array of mechanisms than OWAs to express, maintain, and/or strengthen bonds outside the breeding season. One reason for this may be species differences in social tolerance.

A significant difference was found between OWA and BGM composite social tolerance scores, with results indicating that OWAs showed greater tolerance towards their preferred partners than BGMs. Although neither the agonistic nor the approach tolerance indices were significantly different between species when considered individually, there was a trend for OWAs to direct less of their aggression towards their partner in comparison to BGMs. Furthermore, within species analyses revealed that while OWAs directed significantly less aggression towards preferred partners than other flock members, BGMs did not; no significant difference was found in BGMs in this respect. However, BGM focal birds, like OWAs, did show significantly greater tolerance of approaches by preferred partners than non-partners.

The between species differences that were found in social tolerance suggest that, overall, BGMs demonstrate lower levels of social tolerance to their close social partners than OWAs. This propensity coupled with a beak that is one of the most powerful in the avian world (in terms of crushing capacity, Wade, 2002), means that behaviours that reduce tension and re-establish bonds could be highly adaptive in terms

of avoiding severe injuries. Courtship feeding and vent allopreening may represent such behaviours in BGMs.

In terms of reinforcing the pair bond, vent preening may be particularly effective, as it may be indicative of a high level of trust between individuals. The vent is a highly sensitive body region and some avian species target this area during agonistic encounters (Hughes & Duncan, 1972). Therefore, allowing preening of this part of the body may signal trust; likewise, allopreening a partner's vent without inflicting injury may communicate motivation to maintain an affiliative relationship.

The fact that vent allopreening was observed in BGMs, but not OWAs, was not the only between species difference that emerged in analyses of allopreening. Although OWA focal birds had more allopreening bouts with their partners than BGMs, BGMs spent more time overall engaged in allopreening interactions with their partners. OWAs dyads were found to engage in head allopreening significantly more than body allopreening, which I had predicted for both species (as self-preening of the head is not possible). No difference was found between head and body allopreening for BGM dyads, despite a medium effect size; it is possible that significantly more head allopreening may be observed than body allopreening with a larger sample size. Between species differences were additionally found in the body regions focal birds and their partners focused on the most when allopreening. BGMs engaged in significantly more body allopreening than OWAs. This difference can likely be explained by the presence of preen glands in BGMs and its absence in OWAs; it may also help to explain why head and body allopreening duration were not significantly different in BGMs. BGMs have uropygial glands (also known as preen glands), which are absent in OWAs (Vincze, Vágási, Kovács, Galván, & Pap, 2013). These 'nipple-like' glands excrete oil that has plumage maintenance and ectoparasite functions, and

has to actively be spread throughout the body by preening (Clayton et al., 2010; Zhang, Wei, & Zhang, 2008). OWAs, in contrast, rely on the presence of powder down, which is secreted throughout the body (Vincze et al., 2013). This anatomical difference is consistent with reports of macaw species allopreening all body regions, and Amazon parrots focusing allopreening on the head and neck (Harrison, 1994; Pitter & Christiansen, 1997; Seibert, 2006). These findings raise questions about the types of hygienic versus social functions that allopreening different body regions may serve.

BGM dyads were found to engage in mutual allopreening significantly more than OWA dyads, which research on chimpanzees suggests may be indicative of greater bond strength in BGMs compared to OWAs. Fedurek and Dunbar (2009) found positive correlations between levels of mutual grooming displayed by chimpanzee social partners and relatedness and tendency to maintain close physical proximity. Mutual allopreening was found to be correlated with composite affiliative scores only in OWAs and not in BGMs. It is possible that the greater occurrence of mutual allopreening in BGMs as compared to OWAs may be related to species differences in body size. BGMs are larger, with longer body lengths and longer necks; these physical differences may make it more possible for BGM pair bonds to simultaneously preen one another (see Chapter 3). If mutual allopreening in BGMs is an easy, low cost activity, this may explain why it is not a predictor of composite affiliative scores. In contrast, mutual allopreening may need more coordination and physical effort in the smaller bodied, shorter necked OWAs, and thus be a more costly activity only engaged in infrequently by closely bonded dyads. This may explain why mutual allopreening positively correlated with composite affiliative scores in OWAs. Importantly, this finding indicates that mutual allopreening measures may serve as good indicators of bond strength in OWAs, as appears to be the case in chimpanzees.

Synchrony/coordination indices were not found to be significantly different between OWA dyads and BGM dyads. The fact that OWA pairs are known to engage in ritualised courtship displays (Hoppe, 1992) suggests that greater coordination/synchrony of behaviour may have been observed amongst OWAs had the study group consisted of breeding pairs (as courtship displays are most commonly observed shortly before or after mating, Hoppe, 1992). It would be valuable for future psittacine researchers to further explore species variation in this behavioural category. Coordination and synchrony have been identified as being cognitively demanding, and are believed to have been influential in the emergence of cognitive complexity in birds and dolphins (Emery, Seed et al., 2007; Fellner et al., 2006). Thus, identifying species variation of coordination and/or synchrony in psittacines could allow for these hypotheses to be tested.

Evidence of agonistic support was found in this study, however it was surprisingly rare: just two OWA and BGM focal birds showed aggression towards individuals that had directed aggression towards their closest neighbours. It may be that OWAs and BGMs in highly competitive social environments (e.g. competing for and defending a nest cavity) would be more likely to express agonistic support than the birds observed in my study. However, studies of group-housed rooks and ravens in captive aviaries comparable to the parrots in this study, have found much higher levels of this behaviour, indicating agonistic support may be more prevalent amongst some corvids than BGMs and OWAs (Emery, Seed et al., 2007; Fraser & Bugnyar, 2012).

Evidence of same-sex pair bonds was found in both species; twenty one percent of OWA focal birds and 45% of BGM focal birds were found to have same-sex preferred partners. These results are consistent with various studies of captive, group-housed birds (Abbassi & Burley, 2012; Emery, Seed et al., 2007; Fraser & Bugnyar,

2010; Tomaszycski & Zatirka, 2014), though their significance is unclear. In captive situations the ratio of females to males may be uneven; this was the case in the present study. In such cases, once male-female pair bonds are established, the remaining individuals are left with two options - either be a 'loner' or establish a pair bond with an individual of the same sex. Hardy (1963) found that the establishment of a pair bond was associated with social rank, and while members of opposite-sex pair bonds appeared to have a higher social rank than members of same-sex pair bonds, same-sex pair bonds had higher social rank than birds that had not established pair bonds. It is interesting, however, that such a large portion of BGM focal birds had same-sex partners, considering that these dyads had been selected from a flock that was comprised of more than 100 individuals. One would imagine that they would have had a lot of opportunity to establish opposite-sex pair bonds (with the exception of the male-male pair that had come from quarantine and had been housed there as a dyad). However, as the male to female ratio of this larger flock is unknown, this assumption cannot be tested. It should be noted, however, that no female-female pair bonds were identified in either the OWA or the BGM group. The fact that focal sex was not found to be associated with composite affiliative scores (across species), indicates that differences in level of energy invested by males versus females is not a likely explanation for why no female-female pair bonds were found.

Studies of captive zebra finches and ravens report greater stability of male-male partnerships as compared to female-female partnerships (Fraser & Bugnyar, 2010; Tomaszycski & Zatirka, 2014); it is possible that similar dynamics may exist in parrots. In these studies, finch and raven male pair bonds were more likely to maintain partnerships throughout study periods than female pair bonds, even when given the opportunity to interact with other individuals (including birds of the opposite sex). It is

possible that in OWAs and/or BGMs, female-female partnerships may occur, but may be short-lived if individuals have the opportunity to re-pair with other birds. If this pattern occurs in psittacines, as it does in other birds, it would be intriguing given findings on human sexuality; male sexual orientation has been found to be less flexible than female sexual orientation (Baumeister, 2000; Chivers, Seto, & Blanchard, 2007). As studies of same-sex partnerships have provided insight into the adaptive value of such relationships in varying social contexts (Bailey & Zuk, 2009), pursuing this avenue of study in psittacine research may contribute to our understanding of the evolution of homosexual behaviour. Presently, very little is known about the extent to which psittacines establish and maintain same-sex pair bonds; this is particularly true for wild birds, as the majority of parrots (including OWAs and BGMs) do not show sexual dimorphism.

While this study's findings indicate that OWAs and BGMs are socially complex, forming partnerships that are actively maintained through various forms of affiliative behaviours, they also illustrate the tremendous need there is for further research. One of the major limitations of this study is that it is unclear to what extent housing conditions may have played a role in the similarities and differences that were observed in OWA and BGM social interactions. For example, the fact that most OWAs had positive scores with more than one social partner, while BGMs did not, may be explained by BGM sampling procedures (rather than reflecting a true species difference). The BGM study group was comprised of affiliated dyads and single individuals that had been selected from a very large group-housed flock, or joined the group after having been in quarantine due to being new zoo arrivals. In contrast, the OWA study group had been housed together for at least six months (and in some cases years). The fact that BGMs had less time to adjust to the social composition of their

flock, as compared to OWAs, and other established affiliative partners may have remained in the large BGM aviary, may have contributed to this finding. Future research is needed to establish if my findings are representative of species differences, with OWAs perhaps developing a larger number of affiliative partnerships than BGMs, or an artefact of the differing histories of our two study populations.

Findings obtained in this investigation also illustrate the need for research that addresses the functions of individual affiliative behaviours in psittacine pair bonds (e.g., courtship feeding and the various forms of allopreening interactions). The impact of social tolerance levels, and how aggression is managed between partners, also requires further attention. These factors should be investigated at both the between and within species levels, as well as in different dyad compositions (e.g., same-sex as compared to opposite-sex pair bond or breeding as compared to non-breeding pairs). By doing so, we may gain a better understanding of how affiliative and agonistic behaviours impact the strength of the pair bond, as well as individual fitness. Furthermore, the identification of between species differences may also guide efforts aimed at investigating the association between relationship quality and cognitive factors. In this study, for instance, a great deal of variance was observed in the composite affiliative scores focal birds had with preferred partners; it is possible that such variation may be associated with differences in cognitive ability, as processes such as attention, memory, or inhibitory control may affect how well individuals maintain affiliative relationships. This avenue of research is explored in the following chapters; correlational analyses are reported, which investigate whether performance on cognitive tasks was related to scores OWAs and BGMs obtained on relationship quality measures.

In summary, decades of comparative research have yielded substantial and compelling evidence of complex social relationships across a range of species. The significant associations that have been found between the nature of those relationships and brain and cognitive adaptations, as well as individual fitness and reproductive success, illustrate the importance of expanding relationship quality research. As this study shows, psittacines are ideal subjects for this avenue of research. OWAs and BGMs exhibited various affiliative behaviours, which have been observed in socially complex animals, including primates, dolphins, and other birds. Support was found for the idea the psittacines establish pair bonds, which they actively maintain outside the breeding context. This study, which is one of a limited number of comparative investigations of psittacine pair bonding, also illustrates the value of using a variety of relationship quality measures. Few psittacine studies, for instance, have measured energy invested in allopreening different body regions; by doing so, I was able to identify within and between species variation that may have otherwise been missed. It is only by identifying and exploring such variation that a true understanding of the complexities of psittacine pair bonding can be developed.

CHAPTER 5: PHYSICAL COGNITION

Abstract

Although relatively few parrot species have undergone cognitive testing, initial findings suggest they possess complex cognitive capacities. The studies presented in this chapter are aimed at contributing to our understanding of psittacine cognition. Three experiments are reported in Study 1 which investigate physical cognition in OWAs and BGMs: two measuring inhibitory control using a transparent apparatus task and an A not B task, and one measuring subjects' understanding of connectedness using a two-choice string pulling task. In Study 2, relationship quality (both species) and boldness (only BGMs) are investigated as potential covariates of cognitive performance. Evidence of inhibitory control was found in both species in subjects' performance in the cylinder task. OWAs were found to perform significantly better on cylinder test trials than BGMs. OWAs and BGMs performed poorly in the A not B task, failing to search in the correct cup at above chance levels. Performance was also poor in the string pulling task; none of the BGMs ($N = 9$), and only two of 12 OWAs, met criterion on discrimination training trials. OWAs did not perform above chance on transfer trials, indicating failure to acquire the concept of connectedness. OWA composite cognitive scores (based on scores obtained on the cylinder task and string pulling discrimination training trials) showed a non-significant trend towards being higher than BGM composite scores. Scores on cognitive tests were not found to be significantly correlated with relationship quality scores (based on findings reported in Chapter 4) in either species or across species. BGM cognitive scores were not found to be significantly correlated with overall boldness scores (based on latency to approach objects in 5 tests), but there was a trend for birds with quicker approach times to the object that elicited most uncertainty in the group to have higher cognitive scores.

Results from the OWA inhibitory control study were published in MacLean et al. (2014).

Introduction

Psittacine characteristics (e.g., brain morphology, socio-ecology, life span) suggest that they may have experienced similar cognitive adaptations as have been found in corvids, primates, and dolphins (see Chapters 1 – 4). Thus far, there appears to be support for this notion (see Chapter 2). However, relatively few species have been studied (see Chapter 1). Determining the extent to which cognitive complexity characterizes the Psittaciformes order will require a significant expansion of parrot research, including a wide range of species, investigating various aspects of cognition. The original research I present in this chapter contributes to this effort.

In Study 1, I present experimental studies of OWA and BGM physical cognition, assessing performance on three tasks (two measuring inhibitory control, one measuring causal understanding). Analyses of potential covariates of cognitive performance are then provided in Study 2; performance on tasks was compared to scores experimental birds obtained on relationship quality measures (see observational study, Chapter 4). Additionally, an experimental study on boldness in BGMs is reported, which investigates the potential association between this individual trait and cognitive performance.

Study 1: Physical cognition

Introduction. As discussed in Chapters 1 and 2, the relationship between behavioural flexibility and high-level cognition has been widely recognized by comparative researchers (Emery & Clayton, 2004; Humphrey, 1976; Roth & Dicke,

2005; van Horik, Clayton, & Emery, 2012). The capacity to adjust behaviour in response to newly acquired information, such as when individuals use previous experience to solve novel problems, has been argued to be indicative of flexible cognition that may support some form of logical thinking (Emery & Clayton, 2004; Humphrey, 1976). Central to behavioural flexibility, and associated with high-level cognition, is the capacity to exercise self-control. Inhibitory control is essential to flexible problem solving, and is linked to complex cognitive capacities, such as causal understanding (Carlson, Moses, & Breton, 2002). Both of these capacities, inhibitory control and causal (or ‘means-end’) understanding, have been widely investigated by comparative researchers. The experiments I present in this chapter contribute to that body of research. First, a review of relevant research is provided, focusing on experimental paradigms and study findings that are most relevant to the original research (Experiments 1-3) I present in this Study.

Inhibitory control. Widely recognized as a component of executive functions, inhibitory control is believed to play a critical role in effective problem solving; being able to suppress impulsive or conditioned responses, for instance, makes it possible for individuals to abandon ineffective responses and try alternate (more effective) strategies (Amici, Aureli, & Call, 2008; Dowsett & Livesey, 2000; Willoughby, Kupersmidt, & Voegler-Lee, 2012). Behavioural control thus affords the opportunity to modify behaviour based on newly acquired information, allowing one to adapt to changing circumstances (Bond, Kamil, & Balda, 2007).

As noted in Chapter 2, inhibitory control has been investigated in a range of birds, with studies yielding evidence of positive correlations between task performance and brain size and social complexity. In one of the earliest comparative investigations of avian behavioural flexibility, Gossette and colleagues (1966) tested four species

using a serial reversal learning task (White Leghorn chickens, Bobwhite quails, yellow headed parrots, Red-billed blue magpies). After meeting criterion (18/20) in a spatial discrimination task, reward contingencies were reversed, and the process was repeated. Birds completed a total of 29 reversals. Researchers measured number of errors made, number of sessions it took to complete reversals, and number of initial errors (errors before a correct response). While all species showed improvement in performance with each reversal (in each measure), parrots and magpies significantly outperformed chickens and quails, with magpies showing the best performance. Using a similar reversal task, Bond and colleagues (2007) further investigated behavioural flexibility in corvids. The authors explored the idea that behavioural flexibility results from adaptations to highly complex and unpredictable environments, testing three closely related species that varied in social and ecological complexity (pinyon jays, known to live in stable groups and maintain relationships with several individuals; Clark's nutcrackers, considered relatively asocial and known for their remarkable ability to locate thousands of cached seed across vast distances; western scrub jays, considered dietary generalists and known to show within species variation in social structure depending on the ecological environments populations inhabit). Performance on two-option colour and spatial discrimination tasks was assessed across 20 serial reversals; pinyon jays were found to significantly outperform the other species. This finding, the authors argue, provides support for the idea that an evolutionary association exists between behavioural flexibility and social complexity.

Evidence of behavioural control capacities in corvids and psittacines has also emerged from studies using delayed gratification tasks (Auersperg, Laumer, & Bugnyar, 2013; Hillemann, Bugnyar, Kotrschal, & Wascher, 2014). In these tasks, subjects' ability to postpone consumption of readily available food in favour of a more

valuable, but delayed option (in terms of quality or quantity), is tested. Crows and ravens were tested using accumulation (reward quantity was increased over time) and exchange tasks (an initial food item could be exchanged for a food reward that was of greater value in either quality or quantity). Both species showed the capacity to delay gratification when the delay led to a food reward that was of higher quality, but not when it led to a greater quantity (Hillemann et al., 2014). Similarly, Goffin's cockatoos that were tested on exchange tasks, showed significantly greater performance in the quality condition than the quantity condition. However, the longest cockatoos were able to delay consumption of readily available food was 80s, which is substantially lower than what was reported for crows and ravens (10 min, Hillemann et al., 2014). In the accumulation task, the Goffin's cockatoos showed greater delay capacity (20s) than African grey parrots, who showed a maximum delay of 3s (Vick, Bovet & Anderson, 2010).

While evidence of avian inhibitory control capacities has largely been found using serial reversal or delayed gratification tasks, other inhibitory control research paradigms have been developed and used by primate researchers. One such approach involves the use of a transparent apparatus (such as a plexiglass box) that contains an opening through which food can be retrieved (Amici et al., 2008; Santos, Ericson, & Hauser, 1999). By having a testing procedure whereby the apparatus is baited so that the food is placed directly in front of the subject, but the individual has to reach to the side to access the opening, one can test whether subjects can inhibit the impulse of reaching straight ahead (which would result in making contact with the apparatus's front wall). Using this paradigm, Amici and colleagues (2008) found an association between inhibitory control capacity and social complexity; primate species that have social systems characterized by high levels of fission fusion dynamics (e.g.,

chimpanzees, spider monkeys) outperformed primates with more stable social systems (e.g., gorillas, capuchin monkeys). In addition to using the transparent apparatus paradigm, Amici et al. (2008) investigated inhibitory control capacities using an A not B task. In this paradigm, subjects were presented with an array of possible hiding locations and were required to obtain food from the same location (location A) on several consecutive trials. They were then tested on a displacement trial; subjects were required to search for food after observing it being moved from location A and hidden in an alternate location (location B). It is argued that the repeated reinforcement of searching in location A results in the development of a prepotent motor response, which subjects must inhibit in order to respond correctly (searching in location B) on test trials; subjects that search for food in the previously baited location demonstrate a perseverative error, known as the ‘A not B error’ (Amici et al., 2008; Hoffmann, Rüttler, & Nieder, 2011; MacLean et al., 2014). This error was first identified by Piaget (1954), who used search tasks and displacement tests to investigate the development of object permanence in human infants (see Chapter 2). Several potential explanations for the occurrence of the A-not-B error have been put forth. It has been suggested, for instance, that an individual may perceive the object as being an “integral part” of the original location, lacking the understanding that the object has “its own existence,” while others suggest it is due to working memory that has not yet fully matured (Pepperberg & Funk, 1990, p. 104). More recently, research has focused on the potential role of executive functions, with authors suggesting that this error indicates an immature system, lacking inhibitory control and task-switching abilities (Hoffmann et al., 2011).

Causal understanding. Like inhibitory control, causal understanding is highly adaptive and may be demonstrated through flexible problem solving. Being able to

acquire general principles of causality (identifying the presence of mediating forces that link events), allows individuals to apply previously gained information to new circumstances, and potentially predict or control outcomes in physical or social environments (Visalberghi & Tomasello, 1998). As discussed in Chapter 2, string-pulling tasks have been widely used to test birds' understanding of means-end relationships. One of the causal principles that has been the focus of a large number of avian studies, including parrot research, is that of 'connectedness.' The extent to which birds can acquire and apply this concept has been investigated using multiple choice string-pulling tasks. In a basic set up, for example, two strings would be positioned parallel to one another, with one string connected to food and the other adjacent to food, but not connected to it. Avian researchers have commonly used complex string configurations, varying task features such as the spatial relationship between strings (e.g., crossing them) and perceptual cues (e.g., string colour) (see Chapter 2, Heinrich, 1995; Krasheninnikova, Bräger, & Wanker, 2013; Obozova, Bagotskaya, Smirnova, Zorina, 2014; Schuck-Paim, Borsari, & Ottoni, 2009; Werdenich & Huber, 2006). Parrot species that have performed significantly above chance on tests of connectedness include keas, spectacled parrotlets, and Hyacinth and Lear's macaws (Krasheninnikova et al., 2013; Schuck-Paim et al., 2009; Werdenich & Huber, 2006). The macaw performance reported by Schuck-Paim and colleagues is particularly noteworthy.

The authors used a string-pulling paradigm that had been used by previous avian researchers to test means-end understanding through insightful problem solving (see Chapter 2). They however made an important alteration to the experimental set up of the two-option discrimination test— they controlled for weight and movement. Strings were hung in parallel, vertically from a perch; a table was placed under them, and string ends were laid flat on the table. Subjects were thus prevented (when they

initially tugged on strings) from detecting a difference in weight between a string that was baited and one that was empty, but had food placed next to it; additionally, in this set up, a probative tug did not cause the reward to move (a complete pull was required for the food to move). Both macaw species showed high performance on this test (pulling on baited strings at levels significantly above chance in the first 7 trials). Some individuals (of both species) reportedly selected the correct string on the first attempt and continued to do so thereafter, without tugging on it first. The macaws, they argued, showed the capacity to appreciate the functional elements of the task. However, as the birds did not perform above chance in a condition in which strings were crossed, they acknowledge that additional testing is needed to determine the true extent of their causal understanding capacities. As noted in Chapter 2, ravens and keas have also shown poor performance in the crossed strings condition, despite performing at above chance levels in the parallel strings task (Heinrich, 1995; Werdenich & Huber, 2006). Thus far, the strongest performance on a crossed string condition has been found in spectacled parrotlets (performing significantly above chance in 25 trials, Krasheninnikova et al., 2013).

As indicated above, investigations of causal understanding that aim to identify insightful problem solving by measuring naive subjects' performance upon initial exposure to a task have yielded mixed patterns of results within species (some birds perform very well in some tests, but not others); this has led to a great deal of debate concerning the cognitive significance of high performance, and the extent to which rapid learning may explain results (Seed & Boogert, 2013; Shettleworth, 2010). Research on New Caledonian crows, for instance, has shown that visual feedback plays a critical role as a psychological reinforcer that motivates and sustains the pull-step action sequence until the reward is obtained (Taylor, Medina, Holzhaider, Hearne,

Hunt, & Gray, 2010); crows failed to sustain the pull-step action necessary to obtain the reward when visual access to the string was restricted (the string was suspended through a hole in a horizontally laid board so that it could only be seen when standing directly above it).

It has been argued that instead of measuring spontaneous problem solving by task naive individuals, researchers should use experimental procedures that involve discrimination training and transfer tests; by doing so, one is able to investigate whether subjects are able to acquire a general principle, such as connectedness, and apply it to novel problems (Schmidt & Cook, 2006; Seed & Boogert, 2013). Schmidt and Cook, for instance, first gave pigeons the opportunity to acquire a concept of connectedness through extensive discrimination training using a two-choice task. After meeting criterion, the pigeons were tested on a novel task that used different arrangements of the materials, but exhibited the same means-end relationship as depicted during training. In discrimination training trials, subjects were presented with baited dishes connected to ribbons; one ribbon was continuous and the other was not, containing a gap. In the transfer condition, the ribbons were in the shape of loops, rather than straight strands. While the pigeons showed acquisition of the discrimination task after approximately 150 training trials, their performance on transfer trials yielded no evidence that they had learned about the functional features of the task.

Overview of OWA and BGM experimental studies.

Experiment 1: measuring inhibitory control using a cylinder task. The transparent apparatus paradigm was used for this experiment. The procedure used was the same as was reported in MacLean et al.'s (2014) study, which investigated inhibitory control capacities in a range of animals (including birds, primates, elephants, and rodents) in order to test hypotheses about the evolution of self-control. Data

collected from OWAs in this experiment (as well as Experiment 2, the A not B test) contributed to MacLean and colleagues' data set and findings.

During test trials, OWAs and BGMs were presented with baited transparent cylinders. Subjects had to inhibit impulsive responses based on visual feedback (walking and reaching straight ahead). A correct response consisted of taking a detour to the side of the cylinder where the opening was located. We included an apparatus familiarization phase with an opaque cylinder prior to commencing test trials, as Santos and colleagues (1999) suggest this leads to more accurate estimations of inhibitory control abilities. They found that cotton-top tamarins that gained experience using an opaque version of the transparent apparatus first, and then were exposed to the transparent box for test trials, performed significantly better than subjects that were only exposed to the transparent apparatus. They concluded that the exposure to the opaque apparatus allowed individuals to learn that an alternative strategy, reaching around the side of the box, was a viable option. Subjects were then able to transfer what they had learned to the transparent condition. OWAs and BGMs in this experiment were therefore given 'warm up' trials using an opaque cylinder and required to 'pass' this familiarization phase by meeting criterion before being tested on a transparent cylinder.

Through this investigation, I aimed to: (1) determine whether subjects showed evidence of inhibitory control capacity in their performance on test trials (2) determine whether subject performance improved from the first test trial to the second (after receiving tactile feedback from the transparent material) (3) determine whether performance on training trials and test trials were significantly related (4) determine whether there were between species differences in performance on warm up or test trials.

As large brains and social complexity are characteristics found in parrots, and previous inhibitory control studies have identified associations between inhibitory control capacity and these factors, it is to be expected that inhibitory control capacity is a feature of parrot cognition (Amici et al., 2008; Bond et al., 2007; Emery, 2006; Forshaw, 2006; MacLean et al., 2014). Findings from inhibitory control research on yellow headed parrots and Goffin cockatoos support this assertion (Auersperg et al., 2013; Gossette et al., 1966). OWAs and BGMs were therefore expected to show some degree of inhibitory control capacity.

Subjects' responses in the first and second test trials were compared in order to investigate the possibility that birds may have "initially failed to perceive the transparent barrier," (MacLean et al., 2014, p. 6). Lacking experience with the physical properties of the transparent materials they were tested with, it seemed reasonable that subjects would first attempt to obtain food by completing motor actions consistent with the visual feedback they were receiving (reaching straight ahead). If incorrect initial responses were due to this lack of experience, then the tactile feedback received from an incorrect response would provide individuals with the necessary information to respond correctly in the following trials.

Subject performance in the warm up and test phases were compared in order to explore the possibility that intra-species variability in test performance was associated with perceptual or motor skill.

Experiment 2: measuring inhibitory control using an A not B task. In addition to the cylinder task, we used an A not B task to investigate inhibitory control in OWAs and BGMs. The procedure we used was based on Amici and colleagues' (2008) study: Subjects were required to locate food hidden in one of three cups (cup A) aligned on a table, on three consecutive trials (henceforth referred to as 'simple search trials'); after

meeting criterion, they were each given a single test trial in which they observed the displacement of food and were required to search for it in its new hiding location (cup B). Through this investigation, I aimed to: (1) determine whether subjects showed evidence of inhibitory control (2) determine whether performance on simple search trials was significantly related to test trial performance (3) determine whether OWAs and BGMs performed significantly differently in simple search trials or test trials.

In line with previous findings of inhibitory control in parrots (Auersperg et al., 2013; Gossette et al., 1966), it was predicted that evidence of inhibitory control would be found, with individuals of both species showing the ability to inhibit the A not B error. If subjects showed poor performance on test trials, it was expected that they would search in the previously baited cup (committing the A not B error), rather than searching in the middle cup. In order to explore the possibility that variations in performance on test trials could be explained by variations in motor or visual spatial skills, performance on test trials was compared to performance on simple search trials.

I did not expect to find significant differences between OWA and BGM performance in simple search trials, as there is no reason to believe that there would be interspecies variations in object permanence or learning capacities that would make it easier for one species to acquire the task as compared to the other.

Experiment 3: Measuring means-end understanding through a string pulling task. In order to test OWAs' and BGMs' capacity to understand the concept of 'connectedness,' I followed the discrimination training and transfer test paradigm used by Schmidt and Cook (2006) in their pigeon study. OWAs and BGMs were presented with two baited dishes attached to strings, in a horizontal set up; one string was continuous and the other was not. Materials and configurations used for transfer test trials were highly different. Therefore, if subjects responded correctly on transfer trials

at a level significantly above chance, the findings would provide convincing evidence of the ability to acquire and generalize the causal concept of connectedness. Through this investigation, I aimed to accomplish the following: (1) Determine whether OWAs and BGMs could learn to discriminate between continuous and broken strings (2) Determine whether subjects that met criterion in the discrimination task showed evidence of having acquired the concept of connectedness (3) Determine whether there were significant between species differences in discrimination learning or transfer test performance.

As a variety of parrots, including species closely related to OWAs and BGMs, have performed competently on various configurations of discrimination tests using string-pulling paradigms, I expected both groups to show acquisition of the discrimination task. As this task could be acquired by attending to perceptual features alone, and I had no reason to believe there are perceptual differences between these species that would impact their ability to attend to task features, I did not expect to find interspecies differences in discrimination training performance. It was more difficult to speculate about how subjects would do on the transfer task. As indicated earlier, results for parrot species on tests purported to measure understanding of connectedness have been mixed (Krasheninnikova et al., 2013; Schuck-Paim et al., 2009).

Composite cognitive scores. Composite cognitive scores were created in order to determine whether one species out-performed the other overall. A lack of previous research meant no prediction was made concerning whether one species would outperform the other.

General Methods.

Research site. This research was conducted at Lincolnshire Wildlife Park (see Chapter 4 for details).

Subjects. Inhibitory control and means end experiments were conducted on captive, mixed-sex, group-housed OWAs and BGMs. Further information concerning identification, housing, and diet can be found in Chapter 4.

Data collection period. For both species, training and data collection took place between the months of May and October. OWAs were studied in 2012; BGMs were studied in 2013.

Training/testing compartments. Subject aviaries contained compartments in which subjects were trained and tested (OWA = 1.8 x 1.2 x 2.2 m; BGM = 1.4 x 1.2 x 2 m). Rooms contained tables (OWA = 1.8 m x 61 cm; BGM = 76 x 57 cm), and had trap doors through which birds could be let in and out.

Pre-training. OWAs and BGMs were habituated to my presence and I trained subjects to associate me with rewards by offering them food. This period was used to identify highly valued food items. Subjects were trained to approach and enter testing rooms using an operant conditioning shaping procedure. Initially, food was placed inside the testing room while the door was kept open, allowing interested birds to enter the room to retrieve it from testing tables. OWAs showed a high degree of social tolerance during this process; several birds at a time were therefore initially allowed in the testing room. BGMs displayed high levels of aggression towards non-partners in the testing room; they were therefore only allowed in the testing room one at a time or in partner dyads. As pre-training sessions progressed, length of time birds were kept in the room by themselves increased. If at any point a bird approached the door to leave, or showed any sign of distress, the door would immediately be opened and the individual would be allowed to exit (this was the case throughout all pre-training, training, and testing phases). Pre-training ended when subjects were willing to remain in the testing room (with no other bird present) for a minimum of 5 min at a time.

Training and testing.

Session frequency and duration. One to two experimental training/testing session(s) was (were) held per day, each lasting between 1.5 and 2 hrs. Sessions took place between morning and afternoon feeds. Each subject was allowed to participate in one training or testing session per day.

Procedures. All subjects were habituated to testing apparatuses and rewarded for approaching them prior to all experiments commencing, in order to ensure that poor performance was not the result of neophobic responses to apparatuses. This was done by placing apparatuses and food on the testing table, gradually increasing their proximity to one another. Criterion for habituation consisted of obtaining a food item that was in contact with an apparatus, with little or no hesitation, five consecutive times. Subjects were trained and tested individually, out of other subjects' view in the testing compartment. During test trials, subjects were given 15 s to respond; if they did not, the trial started again. If subjects did not respond in 5 consecutive trials, they were let out of the training/testing compartment and tested at a later point (in the same session or in a following session). All testing sessions were videoed using a Panasonic SDRH40 camera mounted on a tripod. Subject responses were verbally noted as well as recorded on data sheets. Experiments were conducted in the same order for OWAs and BGMs.

Data analysis. Nonparametric tests were used for within and between species analyses due to small sample sizes. As recommended by Field (2009), r values are reported as measures of effect sizes (.10 = small effect, .30 = medium effect, .50 = large effect).

Experiment 1: Measuring inhibitory control using a cylinder task.

Methods.

Subjects. A total of 14 OWAs (five females, nine males) and 11 BGMs (four females, seven males) completed the cylinder task.

Materials. Opaque tubes were used for the warm up trials and transparent cylinders were used for test trials (see Figure 5.1). Different apparatuses were used for OWAs and BGMs due to differences in species size. Cylinders used for OWAs measured 15.2 cm in length and 7.6 cm in diameter. Cylinders for BGMs measured 19 cm in length and 10 cm in diameter. Apparatuses were mounted on wooded bases (OWA: 15.2 x 7.6 x 1.9 cm; BGM: 17.5 x 10 x 5 cm). The OWA opaque cylinder was made of plastic and the transparent one was made of acrylic. BGM cylinders were made of 2 litre clear plastic soda bottles and sheets of white paper were used to line the inside of the cylinders to make them opaque.

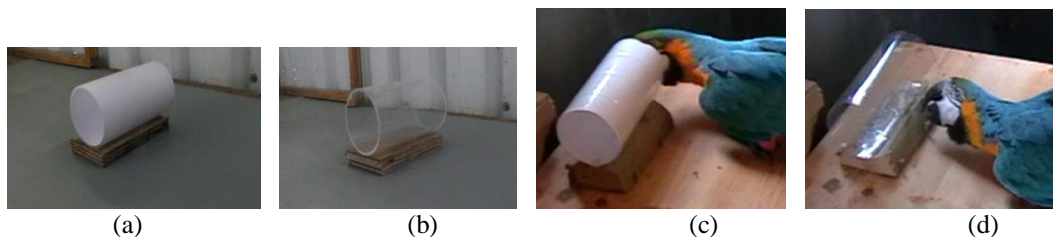


Figure 5.1. Photos of the cylinders used for OWA warm up (a) and test (b) trials, and a correct response during a warm up trial (c) and an incorrect response during a test trial (d) by a BGM.

Procedure.

Warm up trials. The same procedure was used for both species. Each warm up trial began when a subject entered the testing room and stood at one end of the table, facing the apparatus. A food reward was then placed on a tray located between the subject and the apparatus. As soon as it became clear that the subject had focused their

attention on the food reward (looking at it), the experimenter placed it inside the opaque cylinder (approximately a third of the way in). The distance between the tray and cylinder was approximately 30 cm. The subject was then allowed to approach the cylinder and retrieve the food item. If the subject began to approach before the cylinder was baited and the experimenter moved her hand away from the apparatus, the trial started again. The first attempt to retrieve the food was recorded and attempts were coded as correct if the subject walked to the side of the apparatus and retrieved the food from the side opening, without bumping their beak against the front of the cylinder. Attempts were coded as incorrect if the subject attempted to retrieve the food from the front of the cylinder, by contacting it with their beak (see Figure 5.1). Subjects were allowed to retrieve the food on all trials, regardless of whether their first attempt was correct or incorrect. The side from which the cylinder was baited was consistent within subjects and counterbalanced across subjects.

Subjects were required to correctly retrieve food in 4 of 5 consecutive trials before being tested with the transparent cylinder. If subjects left before completing the required number of warm up or testing trials, they were allowed to return during the same testing session and continue from where they left off. If they did not return within the same session, they had to start from the beginning again in the following testing session. Warm-up trials were limited to 10 trials per session. If subjects failed to meet criterion within 10 trials, the session was aborted and subjects started from the beginning in the next testing session.

Test trials. As soon as subjects met criterion on the warm up trials, test trials began. The test procedure was identical to the warm up trials, but the transparent cylinder was used instead of the opaque one. Subjects were required to complete 10 consecutive test trials in the same testing session as the one in which they met criterion.

In cases in which subjects met criterion, but then left the testing room and did not return within that session, they were started on the warm up trials again during the next testing session. This was also the case if subjects completed fewer than 10 test trials in the same testing session; they had to pass the warm up phase again in the following testing session before continuing onto to complete 10 test trials in that session.

Data analysis. The number of sessions and warm up trials it took for subjects to meet criterion, the number of sessions to complete test trials, and the number of correct responses subjects made in test trials, were calculated. For subjects that needed more than one testing session to meet criterion on the warm up trials, the number of trials they required to reach criterion was calculated cumulatively across sessions. For subjects that met criterion, but aborted sessions prior to completing 10 consecutive test trials and later did so in a subsequent session, I calculated both the responses they made in the first 10 test trials they completed (across aborted sessions) and the responses they made in completed sessions; I used data from the former (the first 10 test trials completed) rather than using data from subsequent completed sessions in statistical analyses. I believed this to be a more conservative inhibitory control measure for these subjects as the additional experience they had with the test task prior to completing 10 consecutive trials in subsequent sessions provided them greater opportunity to learn to control primary responses (as compared to subjects that had no aborted sessions after meeting criterion on warm up trials).

A two-tailed Mann-Whitney U test was run to compare species performance, and two-tailed Kendall's tau tests were run to determine whether subject performance during the warm up and testing phases were related. McNemar's test was used to compare subject responses in the first and second test trials to test the hypothesis that

they may have initially failed to perceive the transparent barrier or to recognize the barrier's physical properties.

Results.

Warm up trials. All subjects that participated in this task met criterion in the warm up phase. A Mann-Whitney test showed there was no significant difference between the number of warm up trials that OWAs ($Mdn = 5.5$; $IQR = 4$, $N = 14$) and BGMs ($Mdn = 7$; $IQR = 5$, $N = 11$) required to meet criterion, ($U = 69$, $z = -.46$, $p = .646$, $r = -.09$). OWAs completed between four and 12 warm up trials before meeting criterion; BGMs completed between four and 17. Fifty percent of OWAs and 63.63% of BGMs met criterion within the first testing sessions; all other subjects met criterion in the second or third testing session.

Test trials. It took OWAs between one and three sessions to complete testing (meeting criterion in warm up trials and completing 10 consecutive test trials in the same session). This was also true for BGMs, with the exception of one subject (Mouse), who took seven sessions to complete all test trials. Three OWAs and one BGM aborted sessions after beginning test trials; two OWAs and the BGM had higher scores in completed sessions than in the first 10 trials they completed (including aborted sessions) (see Table 5.1). Although the highest score was obtained by a BGM (90%), a Mann-Whitney test showed that OWAs ($Mdn = 5$; $IQR = 3$, $N = 14$) performed significantly better in the first 10 test trials than BGMs ($Mdn = 3$; $IQR = 5$, $N = 11$), $U = 40.5$, $z = -2.03$, $p = .042$, $r = -.41$. The number of correct responses made by each subject can be seen in Table 5.1.

Table 5.1

Number of OWA and BGM Correct Responses in the First 10 Test Trials and Number of Correct Responses in Completed Sessions for Subjects that Required More Than One Session to Complete 10 Trials

OWA subject	1 st 10 test trials	Completed session	BGM subject	1 st 10 test trials	Completed session
Freckles	7		Elvis	9	
Penny	7		Mouse	6	8
Pete	7	7	Archie	5	
Piglet	7		Digbee	4	
Oliver	6	7	Gizmo	4	
Belle	5		Gwen	3	
Ricky	5		Psycho	1	
Stumpy	5		Lola	0	
Benny	4		Oscar	0	
Bo	4		Red	0	
Joon	4		Sid	0	
Rocky	0	4			
Simon	4				
Tulip	4				

Four OWAs and two BGMs correctly retrieved the food reward on the first test trial they completed. Across both species ($N = 25$), 18 subjects showed no change in response from the first to the second test trials they completed; three subjects changed from incorrect to correct responses, and four subjects showed the opposite pattern. Results from a McNemar test showed that the pattern of change was not significant ($p = 1$; odds ratio = 2.67).

Was performance in the test phase related to performance in the warm up phase? No evidence was found that subject performance in the test and warm up phases were related. Kendall's tau tests showed that the number of warm up trials BGMs ($\tau = -.20$, $p = .446$, $N = 11$) and OWAs ($\tau = -.33$, $p = .151$, $N = 14$) required to reach criterion was not significantly related to the number of correct responses subjects made on test trials. One BGM and four OWAs met criterion, but required additional testing sessions because they did not complete 10 consecutive test trials within the same testing block. Therefore, for these subjects, the total number of warm up trials

they completed was greater than the number of warm up trials they required to meet criterion. The most extreme case of this was Mouse; she met criterion in four warm up trials in the first session, but ended up completing a total of 26 warm up trials across seven sessions before finally completing all required trials within the same testing block (because she repeatedly wanted to leave the testing room before testing was complete). This raised the question, could extra ‘practice’ retrieving food from the warm up cylinder have increased performance in the testing phase? A two-tailed Kendall’s tau test found no evidence of this; the total number of warm up trials BGMs and OWAs ($N = 25$) completed was not significantly related to the number of correct responses they gave during test trials, $\tau = -.09, p = .547$.

Experiment 2: Measuring inhibitory control using the A not B task.

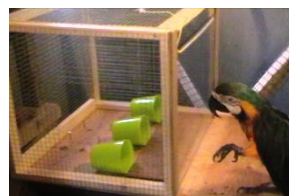
Method.

Subjects. Twelve OWAs (eight males, four females) and 10 BGMs (seven males, three females) completed the A not B task.

Materials. Three opaque plastic cups (OWAs = 7 x 9 cm; BGMs = 9 x 10cm) were used as possible hiding locations for food (see Figure 5.2). A rectangular panel (50.8 x 10.2 cm) was used to prevent OWAs from approaching the experimental set up between trials, and a testing cage (53.6 x 46.5 x 41.6 cm; see Figure 5.2) was used for the same purpose for BGMs.



(a)



(b)

Figure 5.2. Photos of the cups used for OWA (a) and BGM (b) testing.

Procedure.

Habituation. As the three-cup array that was used during simple search and test trials consisted of identical cups, subjects were only exposed to a single cup during habituation (see General Method for description of procedure).

Simple search trials. At the start of each trial, subjects were presented with three empty cups aligned on a table in the open position (on their sides; see Figure 5.2, photo b). As they observed, a piece of food was placed in front of one of the exterior cups (cup A). All cups were then turned over (closed position; see Figure 5.2, photo a), starting with the baited exterior cup. Subjects were then allowed to search for the hidden food (consisting of approaching a cup and touching it with the beak). Subjects were allowed a single choice per trial. Responses were recorded as correct if subjects searched in cup A and incorrect if they searched in the alternate exterior cup or the middle cup. As soon as a subject made contact with a cup, it was placed in the open position, allowing the bird to obtain previously hidden food or to see that the cup they selected was empty. The exterior cup that was baited (left or right) was consistent within subjects and counterbalanced across subjects. Birds were required to respond correctly on three consecutive simple search trials before moving on to the test trial. Subjects were given 10 trials to meet criterion per session. If subjects left the room before meeting criterion or completing 10 trials, they were allowed to resume simple search trials when they returned; they were however required to complete the consecutive trials to meet criterion in the same 'visit' to the testing room. Therefore, if a subject made a correct response before they left the room, they would be required to make three additional consecutive correct responses when they returned (instead of two). Subjects that did not meet criterion in the first session were given the opportunity to do so in subsequent sessions.

To prevent subjects from approaching the three-cup array between trials, barriers were used. A cardboard panel was positioned in front of OWAs and held at chest level. For BGMs, the three-cup array was placed inside a testing cage, behind a transparent plexiglass panel (see Figure 5.2). When experimental set up was complete and it was time for subjects to search for hidden food, panels were lifted and subjects were allowed to approach the cups.

A not B test trial. The test trial procedure that was used followed Amici and colleagues' (2008) procedure. One test trial was given to each subject, and was given immediately after birds met criterion. If subjects left the testing room after meeting criterion, but before completing the test trial, they were required to meet criterion again when they returned. The same three-cup array was used in test trials as was used in simple search trials, and cup A was baited following the same procedure; however, after all cups in the array were closed, subjects observed the experimenter open cup A, take out the food, close the cup, and place the food under the alternate exterior cup (cup B). Subjects were then allowed to search for the food. The first search was recorded, identifying whether birds made contact with cup B, the previously baited cup (cup A) or the middle cup (cup M).

Data analysis. The following were calculated for each subject: the number of sessions they required to complete the A not B task, the number of simple search trials they required to meet criterion, and the number of correct and incorrect responses in simple search trials. For each species, the numbers of individuals that searched in cup A, cup B, and cup M during test trials were calculated. For each species, binomial tests were run to determine whether significantly greater proportions of birds searched in cup B on test trials (responding correctly) than would be expected by chance. The proportions of OWAs and BGMs that selected the previously baited cup were also

analyzed using binomial tests. As subjects could choose from one of three cups on test trials, an expected frequency of .33 was used for binomial tests. Fishers exact tests were run to compare OWA and BGM performance on test trials, including the number of birds that passed the test trials and the number of birds that showed the A not B error. A two-tailed Mann Whitney test was also run to determine whether there was a significant difference in the total number of simple search trials OWAs and BGMs required to meet criterion. A McNemar's test was used to investigate whether subjects that met criterion within the first four simple search trials were more likely to pass test trials.

Results. Approximately half of OWAs completed the A not B task (meeting criterion in simple search trials and completing the test trial) in one test session; of the five that needed additional sessions, two met criterion in the first session, but left the testing room before the test trial could be administered. The maximum number of test sessions any OWA needed to complete this task was four. Seventy percent of BGMs completed the A not B task in one session. The other three BGMs took two sessions to complete the task.

Simple search trials. The number of simple search trials subjects completed before meeting criterion can be seen in Table 5.2; 42% of OWAs and 40% of BGMs met criterion within the first three or four trials they completed. The maximum number of trials a subject needed to meet criterion was 25; this OWA subject scored correctly in the second trial, but showed difficulty responding correctly three consecutive times (his overall correct response rate was 44%). A Mann Whitney test showed that there was no significant difference in the total number of simple search trials it took for OWAs ($N = 12$, $Mdn = 5.5$; $IQR = 4$) and BGMs ($N = 10$, $Mdn = 6.5$; $IQR = 5$) to meet criterion, $U = 55.5$, $z = -.30$, $p = .765$, $r = -.06$.

Table 5.2

Number of Simple Search Trials Subjects Needed to Meet Criterion

OWA subject	Trials to meet criterion	BGM subject	Trials to meet criterion
Freckles	6	Elvis	13
Penny	6	Mouse	7
Pete	9	Archie	3
Piglet	9	Digbee	3
Rocky	5	Gizmo	4
Belle	4	Sid	6
Ricky	3	Psycho	4
Stumpy	3	Lola	8
Benny	6	Oscar	7
Bo	4	Red	11
Simon	25		
Tulip	3		

Test trial. Binomial tests (.33) revealed that significantly smaller proportions of OWAs (.08, $p < .001$, $N = 12$) and BGMs (.20, $p < .001$, $N = 10$) responded correctly (chose cup B) than expected by chance. Only one OWA and two BGMs responded correctly (see Table 5.3). A Fisher's exact test showed no significant interspecies differences in the proportions of OWAs and BGMs that responded correctly on test trials ($p = .571$; odds ratio = 2.75).

Binomial tests showed that a significantly greater proportion of OWAs searched in cup A (.75, $p = .004$) than expected by chance (0.33), whereas the proportion of BGMS that searched in cup A was not (.40, $p = .432$) different from chance. Equal numbers of BGMs selected cup M as selected cup A (see Table 5.3). Although OWAs were 4.5 times more likely to search in cup A than BGMs, a Fisher's exact test showed that this difference was not significant, $p = .192$.

Table 5.3

Number of Subjects that Selected the Correct Cup (Cup B), the Previously Baited Cup (Cup A), and the Middle Cup (Cup M) on Test Trials.

Species	Cup B	Cup A	Cup M
OWA ($N=12$)	1	9	2
BGM ($N=10$)	2	4	4

Is there a relationship between performance on simple search trials and test trial? A McNemar test was run across both species ($N = 22$) to determine whether subjects that met criterion within the first four simple search trials were more likely to pass test trials; no evidence of this was found ($p = .109$; odds ratio = 1.45).

Experiment 3: Measuring means-end understanding using a string-pulling task.

Method.

Subjects. A total of 12 OWAs (four females, eight males) and nine BGMs (three females, six males) completed the means-end task.

Discrimination training and transfer test set up. The same materials and set up were used for both species. Discrimination training stimuli consisted of two white food dishes (2 cm deep, 5 cm in diameter), attached to white strings. In the ‘connected’ configuration, the string was continuous (10 cm long). In the ‘disconnected’ configuration, the string was cut and had a 2.5 cm gap in the middle (see Figure 5.3). Transfer test stimuli consisted of two black loops (10 cm in diameter), made from strands of Velcro. In the ‘connected’ configuration, the food reward (peanut) was placed inside the loop, in contact with the material. In the ‘disconnected’ configuration, the food reward was positioned on the outside of the loop, with a 2.5 cm gap between the food and the loop (see Figure 5.3). Stimuli were positioned inside the

testing cage and were laid horizontally on a grey background. Strings/loops partially extended outside the cage through a 3.8 cm opening at the bottom of the plexiglass, allowing subjects to grasp and pull them.



Figure 5.3. Photos of OWAs responding correctly on a discrimination trial (a) and a test trial (b).

Pre-training. Operant conditioning was used to train OWAs and BGMs to bite and pull on training and testing materials (a string and a Velcro loop). A string or loop was held vertically in front of subjects, along with a food reward. Subjects were required to bite the material in order to get the food. If subjects reached for the food, it was moved away and the string/loop was held closer. If subjects failed to bite the material to gain the reward, the habituation phase was repeated (see general methods). Once subjects had bitten the string and loop on five consecutive trials, they were trained to obtain the ‘connected’ food dish from the cage. It was baited and positioned inside the cage with the string partially extending outside the cage. If subjects failed to successfully pull on the string, the dish was positioned so that it was partially outside the cage and the string fully outside the cage. Subjects were required to pull on the string with little or no hesitation, successfully obtaining food, on five consecutive trials before moving on to discrimination training.

Discrimination training. Sessions consisted of 10 trials. The experimenter used an opaque panel to block subjects’ view while stimuli were arranged. Trials began

when subjects faced the cage and the panel was lifted. Subjects were allowed to ‘select’ one string; a selection was considered to have been made as soon as a bird grasped one of the strings with its beak. As soon as the selection was made, the alternate choice was removed. A response was considered correct if the connected food dish was selected. Connected and disconnected configurations were presented on the left and right side of the testing cage, equally often and in a semi-randomized order; a restriction was used that a configuration could not appear in the same position more than three consecutive times. Criterion to test for transfer was responding correctly in 17 out of 20 consecutive trials (85% across two sessions). OWAs and BGMs were given 150 trials to meet criterion.

Test trials. Subjects that met criterion on discrimination training were given a total of 10 test trials on the subsequent session. The procedure for test trials was the same as for discrimination training trials, except that the transfer test stimuli (black loops) were used (see Figure 5.3).

Data analysis. The number of sessions it took to complete the experiment was calculated for each subject. I also calculated the percentage of correct responses subjects made per session and across all training trials, as well as the number of correct responses made on transfer test trials. Two tailed Mann-Whitney tests were used to compare OWA and BGM performance on the discrimination task, comparing the percentage of correct responses made by both species, as well as the maximum number of correct responses made in one session. A Fisher’s exact test was used to compare the numbers of OWAs and BGMs that met criterion in the discrimination task. For each bird that did not meet criterion, a Spearman’s rank-order correlation was run on the percentage of correct responses they got in each session and corresponding session

numbers. These analyses were conducted in order to determine whether birds showed improvement across training sessions.

Results.

Discrimination training. Two out of 12 OWAs met criterion for testing; Piglet met criterion in 100 trials and Stumpy met criterion in 96 trials. None of the BGMs met criterion ($N = 9$) for testing. A Fisher's exact test showed there was no significant species difference in performance, $p = .486$. All subjects that did not meet criterion completed 150 discrimination training trials, which took OWAs and BGMs between 15 and 17 sessions, and 15 and 18 sessions, respectively. Only one OWA showed evidence of improvement across sessions (analyses excluded birds that met criterion); results of a Spearman's test showed there was a significant positive correlation between session number and the percentage of correct responses that bird made in each session (see Table 5.4). No evidence of improvement was found among BGMs, and one BGM's performance was found to decrease across trials; results of a Spearman's test showed there was a significant negative correlation between session number and the percentage of correct responses that bird made in each session (see Table 5.4).

Mann-Whitney tests showed that there were no significant species differences in the percentage of correct responses subjects made across training trials, (OWA, $N = 12$, $Mdn = 54.93$, $IQR = 6.5$; BGM, $N = 9$, $Mdn = 53.33$; $IQR = 9.34$, $U = 42.50$, $z = -.82$, $p = .41$; $r = -.18$), or the maximum number of correct responses they made in a 10 trial session (OWA, $Mdn = 7$, $IQR = 1$; BGM, $Mdn = 7$, $IQR = 0$, $U = 37.00$, $z = -1.39$, $p = .247$, $r = -.30$).

Table 5.4

Percentage of Correct Responses on all Discrimination Training Trials (N = 150) and Two-Tailed Spearman's Rank Order Correlations for Percent Correct per Training Session (N) and Training Session Number for Birds who did not Meet Criterion = $p < .05$*

OWA subject	Percent correct	n	r_s	p	BGM subject	Percent correct	n	r_s	p
Penny	50.67	17	.53	*.028	Mouse	58.00	17	-.65	*.008
Freckles	58.67	16	.13	.626	Elvis	50.00	16	.12	.662
Pete	56.00	16	-.42	.106	Archie	53.33	15	-.34	.200
Tulip	54.67	15	-.22	.428	Sid	54.00	18	-.35	.158
Belle	58.00	17	-.29	.266	Red	56.67	15	.32	.240
Ricky	52.67	16	-.36	.178	Psycho	57.33	16	-.31	.246
Benny	49.33	15	.20	.484	Oscar	45.33	15	.19	.496
Bo	54.00	16	-.33	.210	Digbee	52.00	16	.22	.424
Rocky	56.67	15	.08	.786	Lola	56.00	15	-.44	.102
Simon	50.67	16	-.28	.288					

Transfer test trials. Both of the OWAs that met discrimination training criterion completed 10 test trials; each in one session (responses can be seen in Table 5.5). Binomial tests (.5) revealed that the proportions of correct responses made by Piglet (.5; $p = 1$) and Stumpy (.7; $p = .344$) were not significantly greater than would be expected by chance.

Table 5.5

Subject Responses on Transfer Test Trials (Correct = C; Incorrect = I)

Trial	Piglet	Stumpy
1	C	C
2	I	C
3	C	C
4	I	C
5	I	I
6	C	C
7	I	C
8	C	C
9	I	I
10	C	I

The creation of cognitive composite scores. As I indicated at the beginning of the chapter, one of the primary objectives of the experimental research I conducted on OWAs and BGMs was to create composite cognitive scores based on subject performance on inhibitory control and means-end tasks. Composite cognitive scores were created in order to determine whether one species showed better overall performance than the other on cognitive tasks.

Data analysis. Although I originally aimed to include test trial scores from all three cognitive experiments, I was unable to do so due to high rates of poor performance by OWAs and BGMs in the A not B and means-end string-pulling tasks; 11 of 12 OWAs, and eight of 10 BGMs responded incorrectly in A not B test trials, so performance on that task was omitted from composite scores. Only two OWAs met criterion in discrimination training (none of BGMs did) and had means-end transfer test trials. As the majority of subjects did not have a score for transfer trials, performance on discrimination training trials was instead used in the creation of cognitive composite scores. Specifically, the maximum number of correct responses subjects made during a string-pulling discrimination training session (out of 10 trials) was added to the number of correct responses subjects made in the first 10 cylinder test trials subjects completed. Due to small sample sizes, a two-tailed Mann-Whitney test was used to determine whether OWA and BGM cognitive composite scores were significantly different. Subjects that did not have scores for both cylinder test trials and string pulling training trials were omitted from the analysis, leaving an N of 12 OWA and 9 BGM.

Results for between species analysis. There was a trend for OWA composite scores ($N = 12$, $Mdn = 13.00$, $IQR = 4$) to be higher than BGM scores ($N = 9$, $Mdn = 9.00$, $IQR = 6$), although a Mann-Whitney test indicated that this difference was not

significant ($U = 27.50$, $z = -1.90$, $p = .057$, $r = -.41$). Individual composite scores can be seen in Table 5.6.

Table 5.6

OWA and BGM Composite Scores on Cylinder Test Trials and Discrimination Training Trials (Score out of a Maximum of 20)

OWA subject	Composite score	BGM subject	Composite score
Tulip	11	Archie	12
Benny	11	Digbee	11
Ricky	13	Elvis	16
Freckles	15	Lola	7
Belle	13	Mouse	13
Piglet	16	Oscar	6
Simon	12	Psycho	9
Rocky	7	Red	7
Bo	11	Sid	7
Pete	14		
Stumpy	15		
Penny	13		

Study 1 discussion. Of the two inhibitory control tasks OWAs and BGMs completed, performance was better in the cylinder task than the A not B task (across both species). This was also the only task in which a significant between species difference in performance was found. Both species, overall, showed poor performance in the means-end task, aimed at testing subject acquisition of the concept of connectedness.

Findings from within species analyses. While some subjects in both groups scored relatively highly in cylinder test trials, OWAs and BGMs did not select the correct cup during A not B test trials at levels greater than expected by chance. Evidence of Inhibitory control capacities was therefore found using the transparent apparatus paradigm, but not the A not B paradigm. Cylinder task results were consistent with previous parrot studies, which report demonstrations of behavioural

control in serial reversal learning and delayed gratification tasks (Auersperg et al., 2013; Gossette et al., 1966). Not all birds, however, did well on the cylinder task; approximately a third of BGMs responded incorrectly on all 10 test trials. No association was found between subject performance during the familiarization phase and subject performance during the testing phase; neither the number of warm up trials it took for subjects to reach criterion, nor the total number of warm up trials they completed, were related to their performance on test trials. This suggests that variations in task performance were not influenced by individual motor or perceptual skills. Therefore, the ease with which subjects are able to successfully retrieve food from a ‘warm up’ apparatus does not appear to be a predictor of whether they will be able to inhibit the impulse of ineffectively reaching for visible food directly in front of them. Similarly, no relationship was found (in either species) between performance on simple search trials and A not B test trials. As such, poor performance on A not B test trials cannot be attributed to task requirements that exceeded subjects’ motor capabilities. This is consistent with findings reported in MacLean et al.’s (2014) large-scale comparative study.

Interestingly, no improvement was found in subjects’ performance from the first to the second cylinder test trial. McLean and colleagues (2014) raise the possibility that subjects may adjust response strategies after obtaining sufficient tactile feedback from transparent testing apparatuses. However, I did not find any support for this (in either species); no evidence was found that the tactile feedback subjects received from incorrect responses on initial trials was necessary or sufficient to change response strategies in second trials. It is possible that some birds in this study performed poorly because there was no real cost to initially responding impulsively. This may be addressed by using a swing-door task, as has been used by primate researchers (Amici

et al., 2008). In this paradigm, subjects are presented with an apparatus containing two transparent doors; a reward is placed behind one door, but not the other. Responding by reaching directly for the food by pushing the baited door causes the reward to fall into a trap. Subjects are instead required to push the alternate door to gain access to the food. This may result in strong enough motivation for subjects to exercise greater inhibitory control, thereby allowing for a more accurate approximation of their true inhibitory control potential.

The fact that 36% of BGMs obtained scores of 0 in cylinder test trials and one BGM got the highest score (90%) (of both species), suggests that while this species has the potential to demonstrate a high degree of behavioural control, differences in individual traits may influence performance on inhibitory control tasks. The variation in BGM performance also underscores the need to be cautious about generalizing findings that emerge from studies with few subjects. Had there only been two or three subjects in the BGM group, a research limitation commonly found in psittacine investigations, this study may have yielded results that would have indicated a complete lack of inhibitory control in BGMs.

Compared to the cylinder task, interpreting the findings obtained with A not B tests is more challenging. Significantly smaller proportions of OWAs and BGMs responded correctly on test trials than expected by chance. Only one out of 12 OWAs and two out 10 BGMs searched the correct cup, with all others searching in cup A or in the middle cup (cup M) instead of searching in cup B. While OWAs showed a tendency to commit the A not B error, with a significantly greater proportion of OWAs searching in cup A than expected by chance, BGMs did not. The same percentage of macaws (40%) searched in the middle cup as in the previously baited cup. As the aim of the simple search trials was for subjects to develop prepotent motor responses, it was

expected that if subjects failed to search cup B, it would be because they engaged in a perseverative response. It is unclear why four BGMs and two OWAs, selected the cup in the middle of the array. Those individuals may have been responding randomly, or may have visually tracked the food's motion across the array, passing cup M, as it was placed in cup B. Their memory of the event may have been complete enough for them to follow the food's general direction, but not complete enough to remember that it was in the cup at the end of the array. It has also been suggested that failure to respond correctly in the A not B task may be associated with limitations in another component of executive functions, task switching abilities (Hoffmann et al., 2011). As successful completion of the A not B task may rely on various executive function skills (working memory, inhibitory control, task switching), it is difficult to determine the extent to which poor performance is specifically due to a lack of inhibitory control capacities. The transparent paradigm, such as was used in the cylinder task, may thus allow for a more accurate measure of inhibitory control.

Performance on the means-end string-pulling task was also poorer than expected. Due to the extensive number of studies that have demonstrated discrimination learning capacities in avian species (Gossette et al., 1966; Herbranson, Fremouw, & Shimp, 2002; Katz & Wright, 2006; Krasheninnikova et al., 2013; Pepperberg, 1987; Smirnova, Lazareva, & Zorina, 2000; Zentall & Hogan, 1978; Zentall, Galizio, & Critchfield, 2002; see Chapter 2), it was very surprising to find that none of the BGMs and only two OWAs were able to meet criterion for testing, despite being given 150 training trials to acquire the task. Additionally, with the exception of one subject, birds that did not meet criterion showed no evidence of improvement across training trials. Based on what is known about parrot learning and cognitive capacities, it is highly doubtful that OWA and BGM failure to meet criterion was the

result of an inability to engage in discrimination learning. It is more likely that poor performance is associated with features of the stimuli and/or set up used during training; for instance, white strings were used against a grey background. Although parrots are known to have excellent colour vision (Knott et al., 2013), the contrast offered by these two colours may not have been sufficient to make the gap of the broken string salient enough for birds to pay attention to.

The above suggestion is supported by findings reported by de Mendonça-Furtado & Ottoni (2008), who reported poor performance by a blue-fronted Amazon on a discrimination test requiring the bird to identify the difference between two pieces of cloth; on one cloth was a slice of banana, while the other piece of cloth was adjacent to a banana slice (pulling on the cloth with the banana on top allowed access to the reward). The subject failed to show task acquisition (criterion was set at 75% in 28 consecutive trials), until the cloth colour was changed from yellow to green. The authors suggest this indicates that the contrast between the banana and the yellow cloth was not sufficient for the Amazon to identify key features of the task. It is therefore suggested that future investigations of OWA and/or BGM discrimination learning use stimuli configurations that provide significant visual contrast. It is also worth noting that the Amazon in Mendonça-Furtado and Ottoni's investigation required over 500 trials to meet criterion in the training phase of the "on" problem. While it is possible that Amazon parrots (and perhaps BGMs) require a substantial number of trials to acquire means-end tasks, it is essential that researchers gain a better understanding of aspects of psittacine visual perception that may impact task performance.

The OWAs that met criterion in the string-pulling task and were tested on transfer trials, showed no evidence of having acquired the concept of connectedness. As indicated in this study's introduction, evidence of causal understanding has been

found in a few parrot species (Hyacinth and Lear's macaws, Schuck-Paim et al., 2009; spectacled parrotlets, Krasheninnikova et al., 2013). However, several other species have shown poor performance on means-end tasks, including tests measuring subjects' understanding of connectedness (e.g., green-winged macaws, sulphur-crested cockatoos, and blue-fronted Amazons; Krasheninnikova et al., 2013; Schuck-Paim et al., 2009). Thus, if causal understanding is indeed a feature of some species' cognitive capacities, it may not be widespread among psittacines. However, relatively few species have been studied, using a limited number of means-end paradigms. Further research is therefore needed before conclusions can be drawn about the extent to which psittacines demonstrate this capacity.

Findings from between species analyses. The only significant difference that was found between OWA and BGM performance on inhibitory control trials was found in the cylinder task, with OWAs showing better performance on test trials than BGMs; the effect size was medium to large, indicating a substantial inter-species difference in performance. As MacLean and colleagues (2014) found that absolute brain size accounted for more inter-species variance on inhibitory control task performance than any other explanatory factor considered (including relative brain size and group size), it was surprising that the larger-brained macaws did not have a significantly greater number of correct responses than OWAs on test trials (BGM brain size = 18.08 ml; OWA brain size = 8.29 ml; Iwaniuk, Dean, & Nelson, 2004).

In the A not B task, both species performed very poorly. In terms of errors made, OWAs were four and a half times more likely to show the perseverative response, although due to small samples sizes this was not a significant species difference. This needs exploring in more detail in a larger sample of both species in order to understand if there is a real species difference in making perseverative errors,

which would have implications for the strength of conditioned responses and behavioural flexibility in the two species. In the means-end string pulling task, OWAs and BGMs were found to perform similarly; no significant differences were found in the percentage of correct responses made on discrimination training trials, or the number of birds that met criterion and moved on to the transfer test.

No significant between species differences were found in cognitive composite scores, although OWA scores showed a trend towards being higher than BGM scores; the medium to large effect size ($r = -.41$) suggests that larger sample sizes may have yielded significant results. This again is surprising given MacLean and colleagues' (2014) finding that cognitive task performance was positively correlated with absolute brain size.

Study 2: Potential Covariate of Cognitive Performance – Affiliative Investment and Boldness

Introduction. Various authors have noted that gaining a true understanding of the factors or conditions that promote complex cognition requires correlational research that compares performance on cognitive tests to specific species characteristics (e.g., social system) or individual traits (e.g., dominance) (Bond et al., 2007; Carere & Locurto, 2011; Cussen & Mench, 2014b; MacLean et al., 2012). As discussed in Chapter 1, hypotheses concerning the evolution of cognition can be tested by investigating a wide range of animals, and identifying socio-ecological or life history factors that covary with specific cognitive capacities (MacLean et al., 2012, 2014). Studies that investigate associations between individual traits and cognitive performance inform this research; for example, potential tradeoffs between patterns of behaviour (e.g., a tendency towards aggression) and the development or expression of

different cognitive skills may be identified; researchers may also find that, in some cases, variation in cognitive performance is better explained by differences in temperament than by differences in underlying cognitive processes (Carere & Locurto, 2011).

In this study, I present correlational analyses that explore potential associations between OWA and BGM performance on cognitive tests (described in the preceding study) and scores they obtained on affiliative measures (based on data collected from the observational study presented in Chapter 4). An experimental study investigating boldness in BGMs is also described, which includes correlational analyses that examine whether BGM boldness scores were related to their performance on cognitive tests.

As discussed in Chapter 1, studies involving many species have found significant positive correlations among brain size, cognitive capacities, and social systems that are characterized by the presence of long-term partnerships (Dunbar & Shultz, 2007, 2010; Emery, Seed, von Bayern, & Clayton, 2007). Dunbar and Shultz (2010) suggest that the emergence of pair bonding among birds played a crucial role in brain size expansion and cognitive development. Such findings led Emery et al. (2007) to propose the relationship intelligence hypothesis, arguing that the establishment and maintenance of a pair bond selects for a type of “relationship intelligence.” They explain that in order for a bonded pair to successfully rear young, and acquire and protect resources, partners must be ‘in tune’ with one another. They are thus faced with the challenge of having to pay attention to their mates’ behaviours, learning about individual characteristics over time in order to appropriately interpret and respond to their mate’s social cues (Emery et al., 2007). Individuals that are skilled at doing so reap the benefits offered by a stable and functional partnership (e.g., cockatiel pairs that had higher compatibility scores outside the breeding season were found to have greater

reproductive success; Spoon, Millam, & Owings, 2006). The relationship intelligence hypothesis therefore proposes that active investment in the maintenance of stable, cooperative partnerships may be associated with flexible, high-level cognitive capacities. Similarities between psittacine and corvid pair bonding complexity and cognitive complexity, support this hypothesis (Emery, 2006; Emery et al., 2007; Dunbar & Shultz, 2010; Zorina & Obozova, 2012; see Chapter 1). While there is substantial evidence that differences in cognitive capacities between avian species may be explained (or influenced) by relationship quality variables, it is unclear whether this may also be the case at the individual (within species) level.

In the first set of analyses that are presented in this study, I investigate whether effort invested in relationship maintenance (see Chapter 4) was correlated with performance on the inhibitory control cylinder task, or performance on the string-pulling discrimination training trials (see Study 1 in this chapter), in OWAs and BGMs. Within species analyses explore the possibility that variation in cognitive performance may be explained (at least in part) by individual variation in the quality of affiliative interactions experimental birds had with preferred partners. Both of the capacities these tasks measured, inhibitory control and discrimination learning, are relevant to relationship maintenance; for example, inhibitory control might allow individuals to be more flexible in their interactions with their partners, and discrimination learning allows individuals to distinguish between partner and non-partner contact calls (Bond et al., 2007; Watanabe & Jian, 1993). In addition to within species analyses, I compared relationship affiliative investment and cognitive performance across species. Combining data from these two study groups was deemed appropriate as no significant between species differences were found in composite affiliative investment scores (see Chapter 4), or composite cognitive performance scores (although there was a trend for

OWA composite cognitive performance scores to be higher than BGMs; see Study 1 this chapter). It was also reasoned that by increasing sample sizes, statistical power would be improved. No a priori hypotheses were made concerning the results of these analyses due to the lack of previous research which examines potential relationships between individual variation in affiliative behaviour and cognitive capacity in birds. There is, however, reason to believe that individual differences in traits (independent of sex and age) may influence (or be influenced by) cognitive variation.

A range of studies have demonstrated that individuals of the same species show behavioural variations that are “consistent across contexts and time;” it has thus been argued that animals possess characteristics that are akin to human personality traits (Carere & Locurto, 2011, p. 491; Frost, Winrow-Giffen, Ashley, & Sneddon, 2007). Furthermore, significant correlations have been reported between individual characteristics and task acquisition, demonstrating that animal ‘personality’ traits are relevant to interpretations of cognitive findings. In avian research, one trait that has been studied in various species is the tendency to engage in active exploration of novel environments and/or objects (Range, Bugnyar, Schlogl, & Kotrschal, 2006; Guillette, Reddon, Hoeschele, & Sturdy, 2010). Chickadees that were identified as ‘slow-exploring,’ for instance, showed greater behavioural and cognitive flexibility in a task that required the reversal of previously learned category rules (Guillette et al., 2010). Similarly, Range et al. (2006) report that ravens that showed lower levels of object exploration demonstrated faster learning rates in a discrimination task. The degree to which individuals show exploration of novel objects/environments is related to the boldness-shyness dimension of personality. Frost and colleagues (2007) explain that bold individuals are characterized by high levels of activity, risk-taking behaviour, and aggression, whereas shy individuals show the opposite.

One of the most common methods of measuring individual variation in boldness is to test latency to approach novel objects (Bergman & Kitchen, 2009; Fox & Millam, 2007; Frost et al., 2007; Meehan & Mench, 2002; Rockwell, Gabriel, & Black, 2012). This approach has been used, for example, to study the effect of environmental enrichment on fear of novel objects in OWAs (Fox & Millam, 2004; Meehan & Mench, 2002), and to examine the relationship between risk-taking and foraging decisions in Steller's jays (Rockwell et al., 2012). While having a tendency towards boldness may be adaptive in some circumstances, it may be detrimental in others. Individuals that show little fear of novel objects, for instance, may be more likely to identify and exploit novel food sources. However, high levels of boldness may increase the likelihood of behaving impulsively, thereby restricting behavioural flexibility.

In this Study 2, I describe an experimental study I conducted that investigated boldness in BGMs through the use of novel object tests. BGM boldness scores (based on latency to approach measures) were correlated with cognitive test scores in order to examine whether individual variation in this trait may account for variation in performance on the cylinder task and string-pulling discrimination training trials. As avian researchers have found that 'slow-exploring' individuals (associated with shyness) showed better performance in a reversal learning task (Guillette et al., 2010), which are often used to test inhibitory control (see Study 1 of this chapter), BGMs with higher latency to approach times were expected to outperform BGMs with lower latency times in the cylinder task. Similarly, a correlation was expected between performance on string-pulling discrimination training trials and boldness scores; this was based on Range et al.'s (2006) findings, which report faster learning rates in ravens that showed lower levels of object exploration.

Relationship quality and cognitive performance.

Methods. Methods used to collect the OWA and BGM relationship quality data that were used for the analyses reported in this section are described in Chapter 4. Methods used to collect data on cognitive performance are provided in Study 1 of this chapter.

Data analysis.

Composite preferred partner affiliation scores (summary of Chapter 4 data analysis). For subjects and their preferred partners, individual affiliative behaviour indices were standardized within species. These standardized indices were combined to create composite preferred partner affiliation scores (calculated by adding: proximity, allopreening and synchrony/coordination indices; BGM composite scores also included courtship feeding), which were used in this study for within species analyses in order to assess potential associations between relationship quality and cognitive performance for each species.

Composite affiliative investment scores (summary of Chapter 4 data analysis).

A separate set of affiliative composite indices were created ('composite affiliative investment scores') for between species analyses. Composite affiliative investment scores were created by standardizing individual affiliative behaviour indices across species (proximity, allopreening, synchrony/coordination, and courtship feeding indices), and adding scores in each behaviour category for each focal and preferred partner. Composite affiliative investment scores were used to assess potential associations between relationship quality and cognitive performance across species.

Analyses run to determine whether relationship quality and cognitive performance were correlated. As sample sizes were small, Kendall's tau (two-tailed) tests were used for all correlational analyses. Potential associations between

relationship quality and cognitive performance were first assessed for each species. Scores for OWAs and BGMs were then combined and analyses were conducted across species. Specifically, for each species, Kendall's tau tests were run on composite preferred partner affiliation scores and each of the following: the number of correct responses subjects made in the first 10 cylinder test trials they completed, the maximum number of correct responses subjects made during a string-pulling discrimination training session (out of 10 trials), and cognitive performance composite scores (see Study 1 of present chapter). The same correlational analyses were run across species but, composite affiliative investment scores (standardized across species) were used instead of composite preferred partner affiliation scores (standardized within species).

Results.

Within species analyses. Measures of relationship quality and physical cognition were positively related in OWAs and negatively related in BGMs: OWAs that had higher composite preferred partner affiliation scores were more likely to have higher cognitive scores than those with low partner scores, whereas the opposite was true for BGMs. Kendall's tau tests revealed, however, that these patterns were not significant: composite preferred partner affiliation scores were not significantly related to performance on cylinder test trials, string-pulling discrimination training trials, or composite cognitive performance scores for either species (see Table 5.7).

Table 5.7

Kendall's Tau Test Results Comparing Composite Preferred Partner Affiliation Scores to Performance on Cognitive Tasks to Determine Whether They were Related

Species	Scores with composite Preferred partner scores	<i>N</i>	τ	<i>p</i>
OWA	Cylinder task	14	.21	.332
	Means-end training	12	.18	.457
	Composite cognitive scores	12	.30	.184
BGM	Cylinder task	11	-.27	.261
	Means-end training	9	-.30	.311
	Composite cognitive scores	9	-.44	.110

Species combined analyses. Taking data from all birds together, Kendall's tau tests showed that composite affiliative investment scores were not significantly related to performance on cylinder test trials ($N = 25, \tau = -.09, p = .536$), string-pulling discrimination training trials ($N = 21, \tau = -.07, p = .701$), or cognitive performance composite scores ($N = 21, \tau = -.10, p = .561$).

Boldness and cognitive performance.

Method.

Subjects. Nine BGMs completed boldness trials (three females, six males).

Materials. Four novel test objects were used, including a multi-coloured wooden parrot toy (18 x 20 cm), a pink rubber chick that flashed lights (7 x 5.5 cm), a plastic lizard (31 x 12.5 cm), and a remote controlled toy car that lit up when turned on (22 x 9 cm; see Figure 5.4). An opaque painting canvas (46 x 61cm) was used as a test screen to block subjects' view during trial set up. Peanuts, favoured food items, were used as food rewards.



Figure 5.4. Photo of objects used for boldness tests.

Procedure.

Habituation. Subjects were habituated to the test screen (see general method for habituation procedure).

Baseline trials. Before trials began, the test screen was placed on the table, in front of subjects, and in the raised position (blocking subjects' view). A peanut was placed behind the screen (52 cm from the end of the table nearest to subjects). Trials began when subjects were positioned on the perch, facing the screen, and the screen was removed. Trials ended when subjects retrieved peanuts or 10 min elapsed.

Subjects were given a total of five baseline trials (one trial per session, one session per day). If a subject failed to retrieve food on a trial, the trial was repeated in the following session.

Test trials. Following the same set up procedure as was used in the baseline phase, food rewards were placed behind the test screen prior to trials commencing. In addition, a novel object was positioned between the screen and food reward. In each test trial, an object was placed 25 cm in front of the peanut, requiring subjects to walk by it in order to retrieve the food reward. Four objects were used (see Figure 5.4), and subjects were given five test trials. All objects were used once, except for the toy car. In one test, the car remained stationary; in a subsequent test, it was moved once (at the start of the trial) from one end of the table to the other, using the remote control.

Subjects were given a maximum of 15 min to retrieve food rewards; if they did, they

were considered to have passed the test. If a subject did not retrieve the food reward, they were given another test trial in the following session using the same object. If they did not retrieve the food in that trial, they were considered to have failed that test. If a test trial was aborted due to a subject's fearful response (including producing an alarm call, flying off the perch, or attempting to get out of the room), the subject was considered to have failed that test. After subjects completed a test, they moved on to the subsequent test, regardless of whether they passed or failed. However, if a subject's response to an object was extreme and indicated a high degree of fear or stress, they were dropped from the experiment.

I devised an object presentation order that was based on object features that may produce fearful responses in BGMs. As all subjects had had experiences with parrot toys similar to the one used in this experiment, the parrot toy was the first novel object subjects were tested with. Stationary objects that did not light up were believed to be less fear provoking for BGMs than those that moved and emanated lights. The plastic lizard and stationary car were therefore used for the second and third test trials, respectively; the rubber chick and car with motion were used for the fourth and fifth test trials, respectively. However, after two subjects completed Test 2, both showing fearful responses to the lizard, this presentation order was re-examined. Based on those subjects' responses, and the fact that the lizard was realistic looking, the possibility that it would be perceived to be a real and potentially threatening animal by BGMs became a concern. I therefore made the decision to use the lizard on the last test (Test 5) for the other BGMs; the presentation order for the other objects remained the same.

Video coding. Videoed recordings of baseline and test trials were reviewed and subjects' latencies to obtain food rewards were recorded on datasheets. Latency to approach included the amount of time (minutes and/or seconds) that elapsed between

the moment the screen test was removed and subjects had visual access to the food item (and test objects during test trials), and the moment subjects placed their beaks on food rewards.

Data analysis.

Calculation of boldness scores. For each subject, mean baseline latency to obtain food rewards was calculated (across five baseline trials). Scores were calculated for each boldness test subjects completed according to the following: If a subject passed on the first trial of a test object (they were given up to two trials per test object), their score for that test object was their latency to the food reward; if a subject had a ‘no attempt’ on the first trial of a test object, but passed that test object on the second trial, their score for that test object was calculated by adding 15 min (the maximum amount of time subjects were given to obtain food in a trial) to the time it took for them to obtain the food reward on the second trial of that test; subjects that failed a test object (either due to two ‘no attempts’ or because the test was aborted due to fear) were given a score of 30 min for that test object. For each subject, mean baseline latency scores were then subtracted from these latency scores to create boldness scores for each test object. Boldness scores for each test object were meaned to create boldness scores that were representative of performance across all test trials completed (‘overall boldness scores’). Median scores were calculated for each test object in order to determine which test object subjects were most hesitant to approach (‘highest latency test object’).

One BGM completed five baseline trials, but her participation in the study was discontinued because she showed a strong fear response during the first test trial she participated in (as soon the test screen was removed and she gained visual access to the

parrot toy, she flew towards the testing compartment exit door; she was immediately let out). This left eight BGMs who completed trials with all 5 test objects.

Analyses run to determine whether performance on boldness and cognitive tests were correlated. Due to small sample sizes, Kendall's tau (two-tailed) tests were used for all correlational analyses. Tests were run to determine whether highest latency test object scores or overall boldness test scores were correlated with the number of correct responses subjects made in the first 10 cylinder test trials they completed, the maximum number of correct responses subjects made during a string-pulling discrimination training session (out of 10 trials), or cognitive performance composite scores (correct responses in cylinder test trials combined with maximum number correct in string-pulling trials).

Results. With the exception of the BGM whose participation in the study was discontinued, all BGMs completed all five boldness tests. Mean baseline latency scores are listed in Table 5.8. One subject failed all five tests; he did not obtain food in any of the test trials he completed; he remained inside the test compartment for all test trials (he did not approach the door or show signs of fear or stress). There was a great deal of variation in the numbers of subjects that passed each test (see Table 5.9), and the scores subjects got on each test (see Figure 5.5). The lizard test object had the highest median latency score of all test objects. Boxplots illustrating boldness scores can be seen in Figure 5.5.

Table 5.8

BGM (N = 8) mean baseline latency scores (measured in minutes)

Subject	Mean baseline Latency
Red	0.12
Psycho	0.07
Digbee	4.00
Elvis	3.27
Gizmo	0.58
Lola	0.21
Archie	0.33
Oscar	0.11

Table 5.9

The Number of BGMs (N = 8) that Passed Each Boldness Test, Listed by Test Object

Parrot toy	Car	Chick	Car with motion	Lizard
7	3	6	3	2

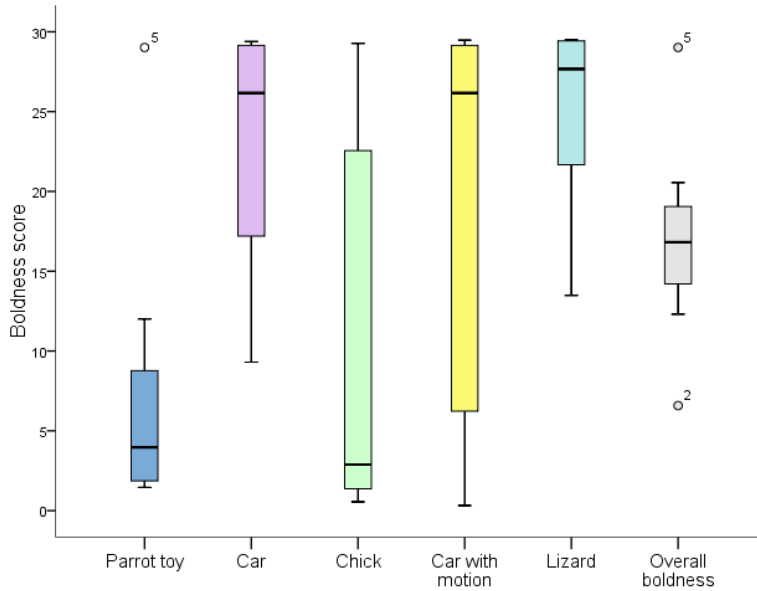


Figure 5.5. Boxplots illustrating boldness scores BGMs got for each object and overall boldness scores.

Were boldness scores correlated with performance on cognitive tests?

Kendall’s tau tests showed that BGM boldness scores (highest latency object or overall boldness) were not significantly related to performance on cylinder test trials, string-

pulling discrimination training trials, or cognitive composite scores (see Table 5.10).

There was a trend for highest latency test object to be negatively related to composite cognitive scores (see Figure 5.6).

Table 5.10
Kendall's Tau Test Results Comparing BGM Boldness Scores to Performance on Cognitive Tasks to Determine Whether They were Related.

Boldness scores	Cognitive scores	<i>N</i>	τ	<i>p</i>
Highest latency test object	Cylinder task	8	-.54	.072
	Discrimination training	7	-.59	.087
	Composite cognitive scores	7	-.59	.068
Overall boldness	Cylinder task	8	.44	.231
	Discrimination training	7	-.07	.849
	Composite cognitive scores	7	.29	.362

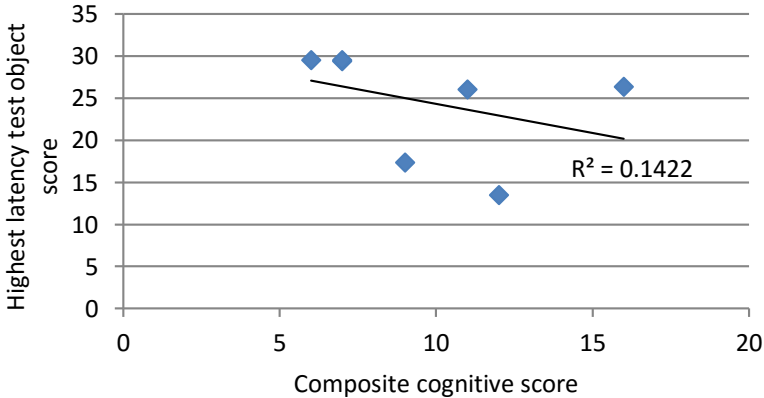


Figure 5.6. Scattergram illustrating the relationship between BGM highest latency test object scores and composite cognitive scores. Line of best fit and R^2 value are illustrated.

Study 2 Discussion. Although evidence of positive correlations have been found between social complexity, including pair bonding, and cognitive complexity, these findings have been at the between species level. To my knowledge, this is the first study that has addressed this potential relationship at the individual level in parrot species. OWAs’ and BGMs’ affiliative investment in relationships with preferred

partners was not found to be significantly correlated with cylinder test trial scores, performance on discrimination training trials (highest number of correct responses made in a session), or composite cognitive performance scores. Therefore, individual differences in the extent to which experimental birds invested and engaged in affiliative interactions (e.g., allopreening) with their partner did not account for the variance observed in cognitive tests.

BGMs showed variation in their performance on individual boldness tests, with boldness scores being highly varied in response to some test objects (e.g., chick and car with motion), as compared to others. Less variation was seen in scores when overall boldness test scores were calculated. Although previous avian research has found that characteristics related to boldness (e.g., tendency to explore) were associated with task acquisition (Guillette et al., 2010), boldness scores in this study were not found to be significantly correlated with BGM cylinder test trial scores, performance on discrimination training trials (highest number of correct responses made in a session), or composite cognitive performance scores. There was, however, a trend for highest latency test object scores to be negatively related to cognitive scores. This was unexpected as a chickadee study reported that birds with higher latency to approach times showed better performance on a reversal learning task (Guillette et al., 2010). It is possible that this association may be present in some avian species, but not others. It would be interesting to replicate this study with a larger sample of BGMs in order to see whether a significant relationship is found. If so, this would refute the idea that boldness increases the likelihood of behaving impulsively, restricting behavioural flexibility.

General Discussion (Studies 1 and 2)

The studies reported in this chapter serve as preliminary investigations of inhibitory control and means-end understanding in OWAs and BGMs, with findings highlighting important methodological issues that should be considered by future psittacine researchers. To my knowledge, the cylinder study provides the first experimental evidence of inhibitory control capacities in OWAs and BGMs (although some evidence of behavioural flexibility has been found in OWA performance in a Hamilton search task, Cussen & Mench, 2014a). In contrast, both species showed overall poor performance in the A not B and string pulling tasks; I believe these findings could be explained by testing procedure limitations than necessarily reflect cognitive limitations.

One factor that must be thoroughly investigated if we are to develop tests that allow us to obtain accurate measures of psittacine cognitive capacities, is the extent to which their visual abilities impact task acquisition. As noted in the discussion of Study 1, colour and visual contrast need to be considered when selecting visual stimuli and stimuli configuration. Lighting source has additionally been identified as something that may influence responses in birds. Although birds have been shown to have overall greater visual acuity than mammals (two to eight times greater), certain aspects of avian visual perception may significantly interfere with their ability to learn about key aspects of a task (Graham, Wright, Dooling, & Korb, 2006; Knott et al., 2013). Graham and colleagues (p. 34) note that “most artificial lights produce noncontinuous light at a frequency of around 100-120 Hz (frames/second),” which produces a “stroboscopic effect” that is perceived by birds (birds and humans detect spatial frequencies of 160 Hz, and 50-60 Hz, respectively). They further explain that artificial lights and sunlight that passes through a window “do not provide full spectrum light.”

The authors therefore advise avian researchers to use light sources that “provide full spectrum light and high frequency sources that emit continuous light” (p. 34).

An additional aspect of the testing procedures used in Experiments 1 – 3 that may have negatively affected OWA and BGM task acquisition was the fact that they were able to immediately respond in training and test trials. This may have allowed them to respond impulsively, without first considering key features of the tasks. Relatively poor performance on the inhibitory control task by several OWAs and BGMs indicates that impulsivity may indeed be high in some of these birds. This limitation can be addressed by including an observation period: de Mendonça-Furtado and Ottoni (2008), for instance, initially positioned test stimuli so that it was within the subject’s (blue fronted Amazon) view, but out of its reach. After 3 s, the Amazon was given physical access to test stimuli. The positioning of stimuli during the observation period also allowed the bird to view the set up from various angles. This procedure (or a similar one) should be used in future OWA or BGM studies to ensure subjects have adequate opportunity to study stimuli before they respond.

Subject living conditions or individual learning histories may have also contributed to cognitive performance. The OWAs and BGMs I used lived in semi-natural conditions. They were group housed, and as such, were able to establish and maintain partnerships. As is reported in Chapter 4, experimental birds were members of pair bonds, and tended to maintain close physical proximity to their partners. The physical separation test subjects experienced from their partners during training and testing may have served as a distraction. Furthermore, subjects lived in relatively stimulating and enriching environments (socially and physically); engaging in physical tasks may not have been particularly rewarding for them. Parrots (or other animals) kept in laboratories (e.g., the African grey ‘Alex’), particularly those housed by

themselves, may demonstrate more focus and interest when given the opportunity to participate in physical tasks. Experimental subjects also had adequate access to varied and high quality food (although food items that were most highly valued were restricted from their diet and used during training and testing); food motivation may not have been sufficient to discourage incorrect responses. The latencies to obtain a peanut in baseline boldness trials were surprisingly high, supporting the notion that these birds were not particularly food-motivated.

In terms of individual learning histories potentially affecting performance, both OWA and BGM subjects were former pets. Although the details of their individual backgrounds are unknown, unfortunately, pet parrots are often housed by themselves in barren environments, with little opportunity to have novel experiences (Meehan & Mench, 2006). A lack of social stimulation or opportunity to engage in object manipulation, as various animal studies have shown, can have substantial negative effects on cognitive development (Davenport, Rogers, & Rumbaugh, 1973; Fox & Millam, 2004; Lapis, Fulford, Muchimapura, Mason, Parker, & Marsden, 2003; Novak, Meyer, Lutz, & Tiefenbacher, 2006).

Although individual variation in affiliative investment was not found to covary with cognitive performance in OWAs and BGMs, this avenue of research is worth further investigation. In the future, pilot experiments should be conducted so that cognitive tasks are less likely to yield floor effects, as seen in two of these tasks. In this study the small amount of variation in subject performance on the majority of tasks reduced the possibility to find meaningful relationships between cognitive performance and individual factors such as boldness or relationship investment. In the future, individual variation on cognitive tasks could be also be correlated with food motivation, executive functions and dominance, which may affect performance.

However, it may also be the case that cognitive complexity in OWAs and/or BGMs is most evident in the social domain, rather than the physical. While physical cognition may not be associated with the demands of maintaining high quality partnerships in these birds, social cognition may be. These issues are investigated in Chapters 6 and 7.

CHAPTER 6: DIFFUSION OF NOVEL FORAGING BEHAVIOUR IN AMAZON PARROTS THROUGH SOCIAL LEARNING

Abstract

While social learning has been demonstrated in several species across many taxa, the role it plays in everyday foraging decisions is less well understood. Investigating social learning during foraging is important as it could shed light on the emergence of cultural variation in different groups. I used an open diffusion experiment to examine the spread of a novel foraging technique in captive Amazon parrots. Three groups were tested using a two-action foraging box, including experimental groups exposed to demonstrators using different techniques and control birds. I also examined the influence of agonistic and pilfering behaviour on task acquisition. Evidence of social learning was found: more experimental birds than control birds interacted with the box and opened it. The birds were no more likely to use the demonstrated technique than the non-demonstrated one, making locale/stimulus enhancement the most likely mechanism. Exhibiting aggression and opening the box were positively correlated, whilst receiving aggression did not reduce motivation to engage with the box, indicating that willingness to defend access to the box was important in task acquisition. Pilfering food and success in opening the box were positively correlated; whereas, having food pilfered did not affect the victim's motivation to interact with the box. In a group context, pilfering may promote learning of new foraging opportunities. Although previous studies have demonstrated that psittacines are capable of imitation, in this naturalistic set-up there was no evidence that parrots copied the opening technique that was demonstrated. Foraging behaviour in wild populations of Amazons could therefore be facilitated by low-fidelity social learning mechanisms.

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Introduction

The instrumental role that sociality is believed to have played in the evolution of intelligence (see Chapter 1) indicates that behavioural and cognitive flexibility are highly advantageous in the social domain (Humphrey, 1976; van Horik, Clayton, & Emery, 2012; Byrne & Whiten, 1997). In a competitive social environment, for instance, the capacity to attend to conspecific behaviour, learn from it, and adjust behaviour in accordance with newly gained information provides significant fitness benefits (Avarguès-Weber, Dawson, & Chittka, 2013; Galef & Laland, 2005). It is thus not surprising that evidence of cognitive convergence is abundant in social learning research, with field and laboratory studies identifying behavioural variations in a range of species that appear to be driven by similar social learning mechanisms.

Discoveries of locale-specific, or group-typical, behavioural patterns among wild populations of animals have been the source of fascination and debate for several decades. They are considered significant because they may reveal evidence of the evolution of culture (Galef, 1992; Laland & Hoppitt, 2003; Moore, 1992). Often referred to as ‘cultural variations’ or ‘traditions,’ regional variations among wild populations have been found in an array of animals, including, mammalian, avian, and fish species (Laland & Hoppitt, 2003; Swaddle, Cathey, Correll, & Hodkinson, 2005; van de Waal, Borgeaud, & Whiten, 2013; van Schaik, Ancrenaz, Borgen, Galdikas,

Knott, Singleton, & Merrill, 2003; Witte & Ryan, 2002; Yurk, Barrett-Lennard, Ford, & Matkin, 2002). These discoveries have led to speculations about the parallels that may exist between the development of animal ‘traditions’ and the emergence of human culture. By conducting research aimed at understanding the spread of novel behaviour in animals, we may gain insight into the cognitive and socio-ecological processes that supported and shaped the evolution of human culture (Galef, 1992; Laland & Hoppitt, 2003).

Social learning provides a way of transmitting a novel behaviour, such as an effective foraging technique, that is more rapid than genetic transmission and more efficient than individual trial-and-error learning. Social learning can occur via a variety of different mechanisms (Whiten & Ham, 1992). Identifying which ones are available to (and used by) different species has important consequences for the potential for faithful transmission and maintenance of new behaviours in a population. The development and maintenance of human culture in particular is believed to rely upon high-fidelity social learning underpinned by imitation, or ‘action learning’ (learning to replicate action patterns through observation) (Legare & Nielson, 2014; Tennie, Call, & Tomasello, 2009; Whiten & Mesoudi, 2008; Whiten, McGuigan, Marshall-Pescini, & Hopper, 2009). This is distinct from emulation (Tennie, Call & Tomasello, 2006), whereby individuals gain information about the function or affordances of an object as a result of another’s actions and consequently achieve the same goal as the observed individual, but may do so by engaging in a different behaviour (Caldwell & Whiten, 2002; Heyes & Saggerson, 2002). In cases of stimulus or locale enhancement, an observer’s attention is drawn to a particular area or object due to another individual’s presence, increasing their chances of approaching and learning something valuable

about that area or object (e.g., learning about the presence of food) (Caldwell & Whiten, 2002).

The two-action test is one of the most widely used paradigms in the experimental investigation of social learning mechanisms, and has been instrumental in helping researchers draw distinctions among stimulus/locale enhancement, emulation, and imitation (Aplin, Farine, Morand-Ferron, Cockburn, Thornton, & Sheldon, 2015 ; Aplin, Sheldon, & Morand-Ferron, 2013; Campbell, Heyes, & Goldsmith, 1999; Dindo, Thierry, & Whiten, 2008; Galef, Manzig, & Field, 1986; Huber, Rechberger, & Taborsky, 2001; Whiten, Horner, & de Waal, 2005). Two-action apparatuses are defined by the presence of two alternative methods through which food may be obtained, such as a pull or push motion, on the same manipulandum (Dindo, Whiten, & de Waal, 2009). If subjects' use of the observed method is significantly greater than their use of the alternate (non-observed) method, it would suggest that rather than just being attracted to the area of the apparatus demonstrators came into contact with, subjects learned something about the technique, either by imitating the actions used or emulating their effects. Further tests (e.g. ghost controls) can be used to dissect the mechanism further (Hopper, Lambeth, Schapiro, Whiten, 2008). It is important to acknowledge, however, that alternate explanations have been offered for high level performance on two-action tasks. Byrne (2003), for instance, argues that action copying may not be due to learning about behaviour, and may not involve any understanding of the actions copied; he suggests that exposure to another individual engaging in an action that is part of an observer's behavioural repertoire may prime neural correlates (e.g., mirror neuron system), thus making the response more available ('response facilitation') and increasing the likelihood that the observer engages in the same action patterns as the demonstrator exhibited.

Although interpretations of high performance on two-action tasks are debated, findings from tests of demonstrator-observer dyads on two-action foraging tasks have provided evidence of social learning in avian, primate, and reptile species that have claimed to be achieved through imitation or emulation (European starlings: Akins & Zentall, 1998, Campbell et al., 1999; pigeons: Zentall, Sutton, & Sherburne, 1996; budgerigars: Heyes & Saggerson, 2002; capuchins: Dindo et al., 2009; chimpanzees: Horner, Whiten, Flynn, & de Waal, 2006; bearded dragons: Kis, Huber, & Wilkinson, 2014; kea: Huber et al., 2001). However, while tightly controlled dyadic tasks may reveal species' social learning capacities, this experimental approach does not reveal anything about the social factors that may influence learning processes within a natural foraging context. Natural foraging parties involve several observers simultaneously being exposed to the same event, who can all then react to the demonstration and potentially become demonstrators themselves. Additionally, behaviours such as pilfering or aggression are highly relevant to the diffusion of novel foraging behaviour in a natural group context. Willingness to tolerate and enter into aggressive encounters, for instance, may ensure sufficient exploration opportunity to acquire behaviour that was previously observed (Schnoell & Fichtel, 2012). Further, gaining rewards from the actions of others may either inhibit social learning (Giraldeau & Lefebvre, 1987) or help focus individuals' attention on demonstrators' actions (e.g., nut cracking behaviour in sub-adult chimpanzees; Inoue-Nakamura & Matsuzawa, 1997). Experimental designs that provide conditions that more closely resemble species' natural social environment are therefore vital for understanding how different types of social learning may function in a more natural foraging context.

The open diffusion design, involving the simultaneous exposure of a group of naive subjects to a trained conspecific engaging in novel behaviour, has greater

ecological validity than dyadic testing (Whiten & Mesoudi, 2008), and has provided further evidence of high fidelity copying in chimpanzees and capuchins (Whiten et al., 2005; Dindo et al., 2009). In contrast, very few studies have used two-action tests to investigate transmission of behaviour through open diffusion in avian social learning research. Examples of such research include investigations of captive and wild tits; in both studies, experimental birds were significantly more likely to use the same solution demonstrated by trained birds than the alternate one (Aplin et al., 2013, 2015). Furthermore, the foraging techniques that were introduced into wild tit populations were found to be stable over two generations (Aplin et al., 2015). This suggests that high fidelity copying could have adaptive value for these birds.

The occurrence of group-specific behaviours in wild avian populations, along with experimental findings that provide evidence of social learning capacities in a range of birds, suggest that avian research can make a significant contribution to the development of a broad comparative framework aimed at understanding the emergence of culture. As discussed in Chapter 1, parrots are often cited alongside corvids as examples of birds that possess high-level, 'primate-like,' cognition (Emery & Clayton, 2004; Emery, Seed, von Bayern, & Clayton, 2007; van Horik et al., 2012). Like primates and corvids, parrots are highly social, have long life histories, and have large relative brain sizes (Seibert, 2006; Shultz & Dunbar, 2010), yet they remain comparatively understudied in most aspects of cognition and behaviour.

In terms of social learning, there is strong evidence that parrots have the capacity for vocal imitation (Bradbury, 2004; Cruickshank, Gautier, & Chappuis, 1993; Hile et al., 2000; Pepperberg, 2006; Rowley & Chapman, 1986; Wright, 1996). However, evidence for imitation of motor patterns, such as those associated with foraging, is less abundant. Moore (1992) reports one single housed African grey parrot spontaneously

imitating non-functional combinations of words and actions from a keeper, in the absence of rewards. In the foraging domain, kea have been found to be capable of stimulus enhancement and likely emulation (Huber et al., 2001), whilst budgerigars were capable of imitating the behaviour of demonstrators (Heyes & Saggerson, 2002). A recent study with Goffin cockatoos showed that whilst they failed to learn to obtain food through novel tool use in a ghost condition, half the birds succeeded when observing a trained conspecific demonstrator. The authors concluded emulation was the most likely explanation for their performance because the tool-using techniques of demonstrators and observers varied greatly (Auersperg et al., 2014), though low-fidelity action-copying mechanisms remain a possible alternative (e.g. programme-level imitation, Byrne (2003)). Psittacines seem to have the capacity to acquire novel motor and foraging behaviour from the observation of others; however, it is unknown what type of social learning occurs in the diffusion of a novel foraging technique in a naturalistic group setting.

The present study aimed to address this issue by investigating the transmission of a novel foraging technique in captive orange-winged Amazon (OWA) parrots (*Amazona amazonica*) using an open diffusion design. As outlined in chapter 3, OWAs, demonstrate characteristics typical of most parrots, including being highly social (see Chapter 4) and having a long life history, a large relative brain size, and a monogamous breeding system (Hoppe, 1992). In the wild, OWAs form foraging parties to locate food sources that vary spatially and temporally (Bonadie & Bacon, 2000). They are also commonly regarded as agricultural pests because they tend to exploit novel food sources as their natural ones are replaced with farm land (Hoppe, 1992). OWAs have vocal mimicry abilities (Hoppe, 1992) and their socio-ecology indicates that it is likely that learning to exploit novel foraging opportunities by

observation of others would be highly adaptive in this species. I tested social transmission of foraging behaviour in OWAs with a two-action foraging box based on the design used by Dindo and colleagues (2008, 2009). Three groups of captive parrots were used. Two of the groups were exposed to group members who were trained to open the apparatus, each using a different technique, while the third group of subjects served as a control group with no demonstrator. I aimed to investigate the following: (1) whether demonstrators' interactions with the testing apparatus influenced whether observers interacted with and solved the task (2) whether successful experimental subjects showed evidence of imitation of observed door-opening methods (slide or pull) or of body parts used (beak or beak and foot) (3) whether, if there was variation in the method used by subjects, they were more likely to conform to using the method of the trained demonstrator, when he was close to the apparatus and (4) whether aggression or pilfering influenced subject engagement with or acquisition of the task.

Methods

Research site. This research was conducted at Lincolnshire Wildlife Park (see Chapter 4 for details).

Design. Three groups of captive parrots were used; two groups of OWAs and one group of blue-fronted Amazons (BFA) (*Amazona aestiva*). One group of OWAs served as the 'slide' experimental group ($N = 22$), while the other OWA group served as the 'pull' experimental group ($N = 15$). Because a third group of OWAs was not available, the 'pull' experimental group was also used as a control group, prior to their experimental trials. The BFAs were used as an additional control group ($N = 20$). This species is very closely related to OWAs, OWAs are known to be neophobic (Fox & Millam, 2004) and anecdotal observation suggested BFAs were bolder than OWAs, I

therefore believed that they would provide a conservative comparison to the experimental groups.

Data collection periods. Data collection on the OWA slide group took place in July 2012. Data collection on the OWA pull group and BFA control group took place in August 2013.

Subjects. All subjects were believed to be adults, though their exact ages were unknown (OWA slide, $N = 22$; OWA, pull $N = 15$; BFA, $N = 20$). Only the sexes of the OWA slide group were known (9 females and 14 males) due to their participation in the observational study reported in Chapter 4. All subjects were identified by coloured leg rings.

Housing and diet. Each of the three groups of parrots was housed in its own outdoor aviary (5.5 x 2.4 x 2.3 m) containing natural wood perches. The enclosures contained covered areas that provided shelter from wind and rain and could be freely accessed by birds. One enclosure had an indoor training compartment (2.2 x 1.8 x 1.2 m), where the OWA slide group were housed in 2012 and the OWA pull group were housed in 2013. Subjects' diets consisted of approximately 70% fresh fruit (fed in afternoon after testing) and 30% seed (fed in morning after testing).

Pre-training. Habituation to three cameras mounted on tripods (see Figure 6.1), as well as an observing researcher occurred for two 30-min periods daily in the two weeks prior to test trials starting. OWAs were trained to enter the training compartment (see Chapter 5 for details). I selected one demonstrator in each experimental group who showed high levels of food motivation, social tolerance, willingness to remain in the training compartment and low levels of neophobia.

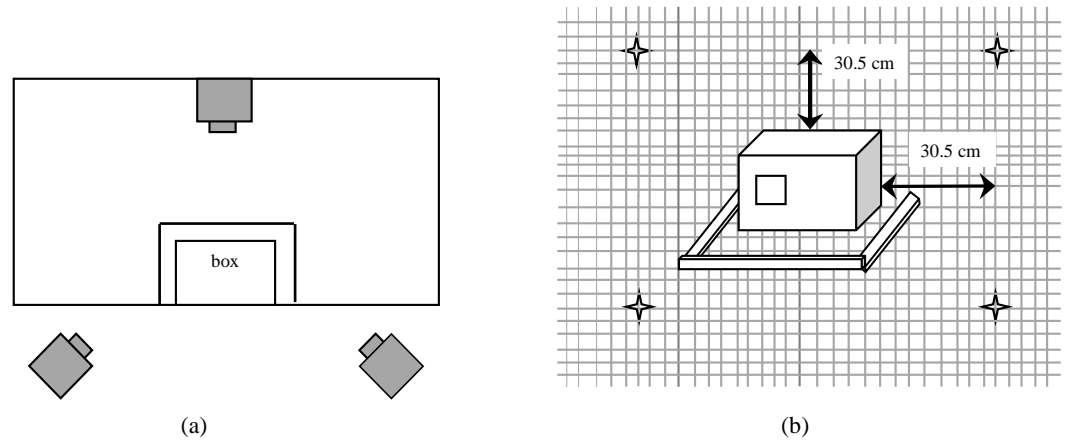


Figure. 6.1. Representations of the experimental setup. A top view of the aviary (a) illustrates the position of the cameras in relation to the box. The camera in the aviary was protected with a camera box. A front view of the experimental box from the parrots' perspective (b) illustrates the position of the U-shaped perch and target zone boundary markers on the mesh in relation to the box

Experimental box

A wooden box measuring 20.3 x 30.5 x 11.4 cm was used as an 'artificial fruit'.

The back of the box contained an opening (20 x 9.5 cm) through which food could be inserted, and the front contained a door (9 x 9 cm) with a handle (1.75 x 4 x 1.75 cm) that could be opened by either pulling it or by sliding it (see Figure 6.2).



Figure. 6.2. Photographs illustrate the foraging box and both methods of opening it - the slide method (a) and the pull method (b)

Training set up. In the training compartment, the foraging box was mounted on the outside of a wire cage (45.7 x 53.3 x 64.8 cm). A T-perch mounted on a base was placed in front of the box door, allowing demonstrators to open the door while standing on the perch. The only birds that were exposed to the training set up were

experimental group demonstrators (trained out of sight of other individuals prior to experimental trials commencing).

Testing set up. Set up was the same for control and experimental trials.

Subjects' first exposure to the testing set up occurred during the first test trial their group completed. The foraging box was placed in the centre of the 'target zone' (TZ) that extended 30.5 cm from all sides of the box. TZ corners were marked with coloured plastic zip-ties or electrical tape so that the boundaries were clearly visible. The box was visually accessible to subjects perched outside the TZ. A U-perch (43.8 x 23.5 cm) was mounted underneath the box (see Figure 6.1). All trials were videoed from three angles using two Panasonic SDRH40 cameras and one Panasonic HCW570 camera (see Figure 6.1).

Procedure.

Demonstrator training. Positive reinforcement and a shaping procedure were used to train demonstrators to successfully open the apparatus door using either the slide or the pull technique. During initial training, the alternate method was locked. Training took place in the training compartment, out of sight of other individuals. If at any point the demonstrators showed an interest in leaving the training compartment by approaching the door or showed any signs of stress, they were immediately let out. Shaping began by first placing food next to the perch and foraging box, requiring demonstrators to approach the items to obtain food. Once they were doing so consistently, the box was baited and its door was kept open (either fully pulled down or slid open). This required demonstrators to step onto the perch and place their heads inside the box to obtain food. After completion of this step, demonstrators were required to move the box door in the target direction, first with the door partially closed and then with the door fully closed. If birds showed difficulty with the final step

(initiating the complete ‘pull’ or ‘slide’ action), it was demonstrated by the experimenter and they were given another opportunity to open the box door. If they were again unsuccessful, they were taken back a step and the procedure was repeated.

Throughout the training procedure, demonstrators were required to fully remove their heads from inside the box prior to it being baited again. Once they removed their heads, the box was re-set and re-baited. The demonstrators were required to successfully open the box in 10 consecutive trials with the alternate door locked before it was unlocked. In order to meet criterion and move onto the testing phase, the demonstrators were then required to open the box using the desired method in 10 consecutive trials, with the alternate method unlocked. Experimental trials began after demonstrators met criterion.

General procedure. Trials began when the foraging box was mounted and baited inside the aviary TZ. Two experimenters stood outside the aviary and provided real time commentary of behaviour in the TZ onto the video recordings (including identifying which individuals entered and exited the TZ and made contact with the box, and describing the type of contact made with the box). One of the experimenters re-set and re-baited the box. The box door was re-set in cases of unsuccessful attempts (see Table 6.1).

Control trials. A total of nine control trials were run on the OWA pull group and the BFAs. As experimental trials would need to be conducted on the OWAs after control trials were completed, the foraging box door was kept locked for the OWA control trials. This was done to ensure that the first exposure that group had to solving the novel foraging task would be as a result of the trained demonstrator’s (TD’s) behaviour during experimental trials. This OWA group was therefore used so that a comparison could be made with regards to level of interest shown in the foraging box,

as opposed to number of successful opens or the method used to open it. The BFA control group allowed for this broader comparison; both options for opening the box door were kept unlocked for their control trials. All control trials lasted 30 min.

Experimental trials. Twelve peanuts and 12 grape halves (favoured food items) were available in each experimental trial. Trials ended when (i) all 24 pieces of food were successfully retrieved from the foraging box or (ii) if 20 min elapsed since the last interaction with the box. In cases in which there was no interaction with the box at all, trials ended after 30 min. I ensured both experimental groups retrieved the same number of pieces of food from the box (216 pieces of food) across all their trials. This resulted in the slide experimental group completing a total of nine trials and the pull group completing 13 trials.

Video coding. The Observer XT 10 program was used to code videoed subject behaviour that occurred within the TZ (see Table 6.1) Methods used for unsuccessful attempts that included both slide and pull actions were coded as ‘slide-pull.’ Methods used for successful attempts that included both slide and pull actions were coded according to whether subjects retrieved food through the opening that resulted from a pull or slide action. Subject attempts were coded as separate behaviours if a minimum of 3 s elapsed between behaviours. This rule also applied to agonistic behaviours involving the same individuals. In cases of unidirectional or mutual aggression, subjects were considered observers if they were not in physical contact with the box door at the start of the aggression; any bird (trained or non-trained) that was in physical contact with the box door was considered a demonstrator.

Table 6.1
Behaviours Coded from the Videos During Social Learning Test Trials.

Behavioural category and behaviours		Definition
Target zone	Inside TZ	50% or more of a subject's body is within the boundaries of the TZ area.
Attempts	Touches box	Subject makes contact with the box; area touched (door handle, front of box, or other part of box (not front) and body part(s) used (beak, foot, or beak and foot) are coded.
	Unsuccessfully opens	Subject partially opens box door; method (slide, pull, or slide-pull) and body part(s) used (beak, foot, or beak and foot) are coded. Subject fully opens box door, but food is pilfered; method (slide or pull) and body part(s) used (beak, foot, or beak and foot) are coded.
	Opens successfully	Subject fully opens box door and retrieves food; method (slide or pull) and body part(s) used (beak, foot, or beak and foot) are coded.
	Fully successful	Subject fully opens box door and retrieves food; method (slide or pull) and body part(s) used (beak, foot, or beak and foot) are coded.
Agonistic	Unidirectional	A subject directs aggression (squawking, pecking, forcing off perch, or raising a foot at another individual) towards another subject; roles of individuals are coded (demonstrator or observer; victim or aggressor).
	Mutual	Two subjects direct aggression (see above) towards each other; roles of individuals are coded (demonstrator or observer). There is an agonistic interaction between two subjects in the context of a successful or unsuccessful pilfering attempt.
Pilfer	Involving pilfering	A subject takes food from inside the box after the box door has been opened by another bird; roles of individuals are coded (victim or pilferer).
	Inside box	A subject takes food from a bird after that bird successfully retrieved it from the box; roles of individuals are coded (victim or pilferer).
	Outside box	A subject takes food from a bird after that bird successfully retrieved it from the box; roles of individuals are coded (victim or pilferer).

To test the accuracy of video coding, a second independent individual blind to the experimental group coded a randomly chosen sample of 6 (2 control and 4 experimental) of the 38 trials (16%) with the full coding scheme (Table 6.1) in Observer XT, and a Cohen's kappa test was run to assess inter-observer reliability. The

mean kappa score was 89.33, indicating a high level of agreement between coders and that the videos had been coded accurately.

Data Analyses. Analyses were conducted using data from nine OWA and nine BFA control trials, and nine experimental trials from the OWA slide group. Only 11 of the 13 experimental trials conducted with the OWA pull group were analysed; in the two excluded trials no bird (neither TD nor subject) entered the TZ. The IBM SPSS Statistics 21 program was used to run the majority of analyses, which were nonparametric due to small sample sizes or because data were not normally distributed. As one of the OWA groups served as both a control and an experimental group, I did not run independent samples tests to compare experimental and control groups in analyses in which OWA and BFA control groups were combined. I instead used binomial tests to compare experimental birds' interest in the box (proportion of subjects that (i) entered the TZ and (ii) that made contact with the box), with expected frequencies derived from control subject performance. As only BFA control birds had the opportunity to open the box (door was locked for OWA control trials), I compared the number of experimental birds that successfully opened the box door to the number of BFA control birds that successfully opened the box door using a two-tailed Fisher's exact test. Two-tailed Wilcoxon signed-ranks tests were run to compare subject use of box door-opening methods, and to compare subjects' attempts 1 min before and 1 min after being victims of unidirectional aggression or pilfering. Kendall's tau tests were run to investigate possible relationships between attempts and agonistic or pilfering behaviour across trials (for both victims and aggressors). As recommended by Field (2009), I report r values as measures of effect sizes (.10 = small effect, .30 = medium effect, .50 = large effect).

I also used a generalized linear mixed-effects model (GLMM) with a binomial error structure to investigate whether the subject door-opening method ($N = 278$ full opens by non-trained birds) matched their respective TD method or not (binary dependent variable) was influenced by the presence or absence (0/1) of the TD in the TZ (categorical explanatory variable). I ran the GLMM in R Version 3.1 and used the package lme4 to run random intercepts models. In order to control for pseudoreplication; subject ID ($N = 10$) and trial number ($N = 16$) were entered as random factors to account for multiple data points being taken from each individual and each trial. To assess the significance of the explanatory variable, I compared the model containing this variable with a null model, comprising only the intercept and random effects, using a likelihood ratio test.

Results

Trained demonstrator performance. Overall, both of the TDs consistently used the trained method to open the foraging box during test trials, although overall the slide TD provided more demonstrations than the pull TD, particularly in the first two trials (see Table 6.2). All of the interactions with the box and successful opening attempts in the experimental groups occurred after demonstrations by the TDs (Table 6.3).

Table 6.2

Box Opens by Trained Demonstrator Across all Trials and in Each of the First Three Trials

Trained method	Total		Trial 1	Trial 2	Trial 3
	Slides	Pulls			
Slide	80	2	11 (all slides)	15 (all slides)	8 (all slides)
Pull	2	66	3 (all pulls)	5 (all pulls)	20 (all pulls)

Table 6.3

Number of Times TDs Demonstrated Before Subjects' First Interactions with the Foraging Box

Type of initial interaction with the box	Demonstrations by Slide TD	Trial in which interaction occurred	Demonstrations by Pull TD	Trial in which interaction occurred
First physical contact	3	Trial 1	4	Trial 2
Door handle touched with beak	7	Trial 1	6	Trial 2
Unsuccessful attempt to open door	8	Trial 1	14	Trial 3
Door successfully opened	17	Trial 2	37	Trial 4

Is there evidence of locale or stimulus enhancement?

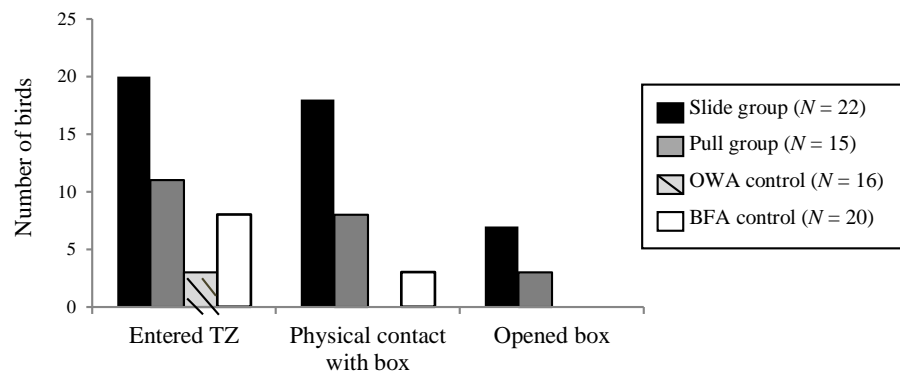


Figure 6.3. Number of birds that entered the TZ, interacted with the box, and opened the box.

To determine whether subjects' interest in the foraging box was influenced by exposure to TDs' successful manipulation of it, the number of experimental and control subjects that entered the TZ, made contact with the box, and opened the box were compared (see Figure 6.3). Using the combined control groups' performance as the expected frequency for the proportion of subjects that (i) entered the TZ (.31) and (ii) made contact with the box (.08), binomial tests showed that the proportion of experimental birds that entered the TZ (0.81; 30/37) and made contact with the box (0.70; 26/37) were significantly above expected levels ($p < .001$). None of the OWA control birds made contact with the box. One BFA control bird made contact with the door handle with the tip of its beak, but did not manipulate the door in anyway. A

Fisher's exact test showed that the number of experimental birds that had successful door-opening attempts (10/37; see Table 6.1 for definitions) was significantly greater than the number of BFA control birds that had successful door-opening attempts (0/20), $p = .010$; see Figure 6.3. As can be seen in Figure 6.4, as the frequency of TD box door opens increased, so did the number of subjects that made contact with the box.

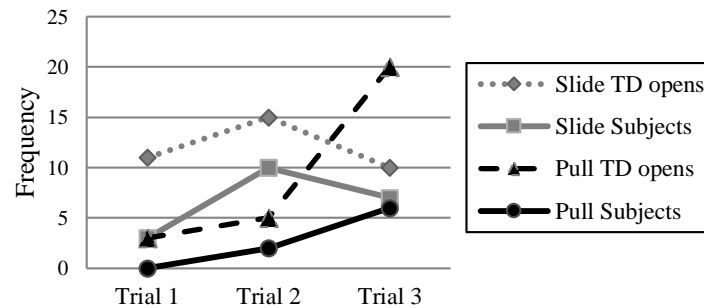


Figure 6.4. Number of demonstrations by TDs and number of subjects that made contact with the box in the first three trials for experimental groups.

Did subjects imitate the door opening methods they observed? The methods used by subjects during all successful opens (including those where the food was pilfered from the bird that opened the box) were compared to methods used by their groups' TDs to determine whether they matched. A two-tailed Wilcoxon signed-rank test showed that subjects that successfully opened the box ($N = 10$) did not use the demonstrated method ($Mdn = 5.50$, $IQR = 22$) significantly more than the non-demonstrated method ($Mdn = 5.50$; $IQR = 40$), $z = -0.36$, $p = .720$, $r = -.11$ (see Figure 6.5); six subjects used both methods to open it. As individuals may have developed a preference for the alternative method through individual learning during the course of the experiment, subjects' initial attempts were also analysed; a binomial test (0.5) showed that the number of OWAs whose first successful open matched the demonstrator's method (6/10) was not above that expected by chance ($p = .754$).

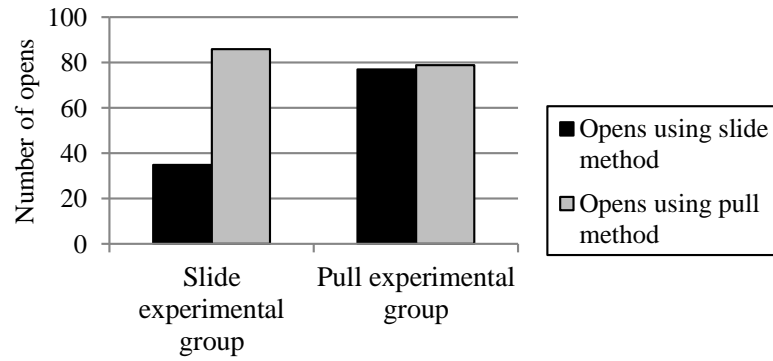


Figure 6.5. Number of times subjects successfully opened the foraging box using each technique. Total number of successful opens in the slide group were 121 and 156 in the Pull group.

I investigated the hypothesis that subjects would replicate their TDs pattern of body part use when opening the box. The slide and pull TDs showed different patterns, with the slide TD using only his beak and the pull TD using both his beak and a foot in the majority of successful attempts. In contrast, subjects in both groups showed a similarly high preference for beak only opens (see Table 6.4). Across both groups the beak only was used in 99% of opens that used the slide method opens and 92% of pull method opens. There was no instance in which a bird used only its foot to open the box door.

Table 6.4

Total opens and percentage of beak only opens per group using each method

Method	Group	Number of opens	% beak only
Slide	Slide TD	80	100
	Slide subjects	35	97
	Pull subjects	77	10
Pull	Pull TD	66	8
	Slide subjects	86	95
	Pull subjects	79	89

I conducted a GLMM to assess if subjects were more likely to conform to the TD's method of box opening when he was present in the TZ. The GLMM indicated that the TD presence in the TZ during or shortly before a subject's attempt did not affect the likelihood of the subject using the box-opening method that matched that of the TD ($X^2(1) = 0.09, p = .761$).

In this open diffusion setting, non-trained birds became demonstrators once they successfully opened the box. As such, I tested whether birds were influenced by the last demonstration they were exposed to before their successful attempts (or first successful attempt if they produced a sequence of attempts without intervening demonstrations from others). A Wilcoxon signed-rank test for the 10 birds that succeeded in opening the box showed that the number of attempts that matched ($Mdn = 4.50, IQR = 17$) the most recently used method by (trained and non-trained) demonstrators was not significantly different from the number of non-matching attempts ($Mdn = 8; IQR = 28$), $z = -1.13, p = .258, r = -.36$.

Did aggression influence subjects' interactions with the box? As the presence of a food source that could be monopolized created a competitive social environment, I examined the role that aggression may have played in subject task acquisition. Agonistic behaviour was seen in all slide experimental group trials and in 10 of 11 trials in the pull experimental group. Both groups displayed similar total instances of aggression (slide group $N = 172$ agonistic events involving 15 individuals (including the TD); pull group $N = 178$ agonistic events involving 7 individuals (including the TD); see Figure 6.6); No aggression was observed in control groups.

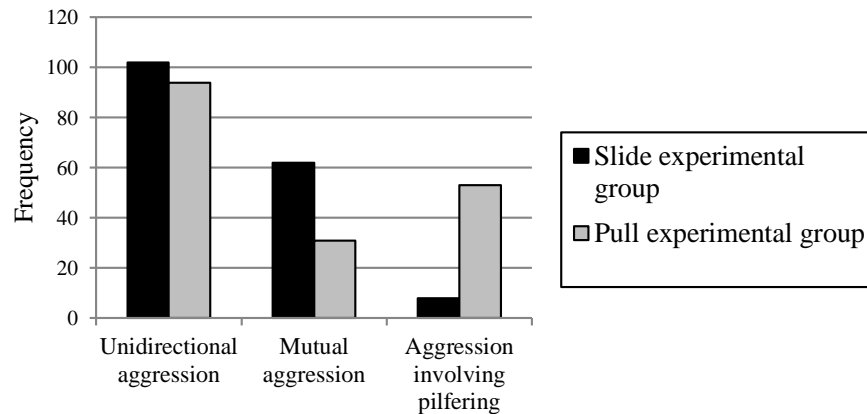


Figure 6.6. Frequency of each type of aggression in each experimental group

In order to determine whether subjects were less likely to make contact with the box immediately after being the victims of aggression, I focussed on the 19 birds who received unidirectional aggression in the TZ (not including TDs). For each agonistic event, I calculated the number of victims' attempts to open the box (see Table 6.1: all categories included except touch other part of box (not front) 1 min before and 1 min after the aggression). For each victim ($N=19$) I then took mean values across all instances where they received aggression. A Wilcoxon signed-rank test showed there was no significant difference between victims' mean number of contacts with the front of the box 1 min before the aggression ($Mdn = 1.00$, $IQR = 1.88$) and after the aggression ($Mdn = 1.00$, $IQR = 1.50$; $z = -.18$, $p = .859$, $r = .04$).

Although receiving aggression did not affect interactions with the box in the short term, I also examined whether the amount of aggression received was related to box interactions across trials. I focussed on birds (except TDs) that were the victims of unidirectional aggression and/or touched any portion of the front of the box for this analysis. Only subjects that had data points for at least one of these two behaviours in seven trials or more were included in this analysis ($N = 6$). I ran correlational analyses for each of these birds individually and despite small sample sizes, Kendall's tau tests

showed significant positive associations between the duration of unidirectional aggression received and the number of victims' attempts to interact with the front of the box for three birds (see Table 6.5). For those OWAs, making more attempts to interact with the front of the box was significantly correlated with receiving more aggression (see Table 6.5). I found no evidence on either a short or long term basis that receiving aggression reduced victims' motivation to interact with the box.

Table 6.5

Results of Kendall Tau correlations between duration of aggression received and number of physical contacts with the front of the box across trials. Analysis only run for individuals that interacted with the box and/or were victims of unidirectional aggression in seven trials (N) or more.

Subject ID	N (trials)	τ value	p value
GYLSR	7	.76	.007
RR	8	.65	.008
PUR	8	.67	.020
RBN	8	.37	.142
LGR	9	.33	.194
OL	9	-.09	.741

An additional analysis was conducted to determine whether there was a relationship between successfully opening the foraging box and giving aggression to other group members in the TZ. All (non-trained) birds that displayed unidirectional aggression and/or successfully opened the box were included in this analysis ($N = 14$), with the total number of successful opens and giving aggression to others events that occurred across all trials entered for each bird. A Kendall's tau correlation revealed a significant positive relationship between the frequency of directing aggression towards others and the frequency of successfully completing the foraging task ($\tau = .52, p = .015, N = 14$ birds).

Did pilfering influence subjects' interactions with the box? As pilfering victims did not benefit from their successful door-opening attempts, while pilferers

gained rewards as a result of others' successful door-opening attempts, I examined whether victims' and pilferers' motivation to interact with the box may have been impacted by this behaviour. A total of 83 instances of pilfering were recorded across both experimental groups (slide $N = 39$; pull $N = 44$) and the majority of these ($n = 63$) involved the pilfering of food from inside the box (slide $n = 33$; pull $n = 30$). To assess whether having food stolen had a short term effect on the victim's motivation to engage with the box, for each pilfering event I calculated the number of times victims (excluding TDs) successfully opened the box door in the 1 min before and 1 min after being pilfered. For each victim ($N = 8$), I then took mean values across all instances where they experienced pilfering. A Wilcoxon signed-rank test showed no significant difference between the mean number of times victims opened the box before they were pilfered ($Mdn = 1.21$, $IQR = 1.00$) and after they were pilfered ($Mdn = 1.75$, $IQR = .62$; $z = -1.36$, $p = .176$, $r = -.48$).

To assess whether across trials successfully pilfering food from another was related to successfully opening the box, I conducted a correlational analysis. All birds (except TDs) that pilfered from inside the box and/or successfully opened the box were included in this analysis ($N = 10$). A Kendall's tau test showed that there was a significant positive relationship between total number of times subjects pilfered food from inside the box and total number of times they successfully opened the box ($\tau = .87$, $p = .001$, $N = 10$ birds).

Discussion

My study provides further evidence of social learning capacities in psittacines, and to my knowledge, is the first to present evidence of this capacity in OWAs in a foraging context. The results obtained indicate that, at the very least, OWAs benefit

from stimulus and/or locale enhancement. Significantly more experimental birds were found to make physical contact with the testing apparatus than controls. This suggests that subjects' interest in the foraging box was increased due to TDs' interactions with it. More subjects in the slide group were found to have approached and touched the box in the first few sessions as compared to the pull group. This is likely due to the greater number of learning opportunities provided by the slide TD in the initial sessions compared to the pull TD. However, some of this variation may also be attributable to the pull group's prior experience as a control group, where they may have learnt the box was an irrelevant stimulus, so they needed more time to overcome this.

Whilst none of the control birds solved the task, 10 experimental birds acquired this novel foraging technique. These findings are consistent with previous avian research, which commonly reports significant differences between experimental and control birds in social learning tests (Fritz & Kotrschal, 1999; Huber et al., 2001; Langen, 1996; Midford, Hailman, & Woolfenden, 2000). It is possible that successful acquisition of the task was influenced by emulation of the demonstrators, in addition to stimulus/locale enhancement: by observing skilled demonstrators, experimental OWAs could have learned about the affordances of the box, in that movement of the box door revealed food. Alternatively, successful performance by the birds that opened the testing apparatus may have relied on trial and error individual learning once they were attracted to the apparatus through stimulus/locale enhancement. Unfortunately, it is not possible to distinguish between the influences of locale/stimulus enhancement and emulation on subject performance in the present study. Future studies that employ two-action paradigms could address this issue by incorporating a ghost condition, in which individuals are exposed to the movement of the door, but with no demonstrator visibly causing them ("as if guided by an invisible ghostly agent," Hopper et al., 2008, p. 835).

This would provide them the opportunity to learn about the affordances of the object. However, while a failure to learn from a ghost control would indicate that social enhancement was necessary for the facilitation effect, it still might not be sufficient. Another possible follow up would be to allow birds to see the demonstrator approach the box and leave with food, but somehow occlude the information about how it opened the door, and see if this provides birds with sufficient information to facilitate learning.

Although my findings provide strong evidence of stimulus and/or locale enhancement and the possibility of emulation influencing subjects' acquisition of the two-action foraging task, no evidence of imitation was found. Both door-opening techniques (slide and pull) were used by OWAs in both experimental groups, and no connection was found between methods used by subjects and methods used by their groups' TDs, either in their overall performance or their very first open (before individual reinforcement for that behaviour had occurred). In this open diffusion setting, other birds who acquired the task then became demonstrators, but there was no evidence that birds copied the method they last observed (from a trained or non-trained demonstrator) before each attempt. In contrast to the recent reports of sensitivity and conformity to the foraging preferences of group members in other species (Aplin et al., 2015; Whiten et al., 2005; van de Waal et al., 2013), experimental subjects in my study showed no inclination to conform to using the TDs' methods when he was present with the subject in the target zone. As both TDs consistently and repeatedly obtained food from the testing apparatus using the method they were trained to use, poor TD performance is not a plausible explanation for the lack of replication of TDs' actions. Although the sample sizes were small for some analyses, the small effect sizes obtained indicate that these are genuine null effects, rather than type 2 errors. Overall, subjects used the pull method about a third more often than the slide method. Despite efforts to

have two actions that were equally easy to execute, it may be that this motion, pulling with the beak, is more similar to actions required for natural foraging such as the extraction of seeds and nuts from hard shells, than the slide action. The slide action was, however, clearly within the capacity of OWA, as 9/10 birds (three from pull group) who learnt to open the box used this method at least once. In the future, researchers may want to consider using more novel actions that are not likely to be used in natural feeding behaviour, but are within the scope of subjects' motor capacities.

As compelling evidence of complex social learning capacities has been reported in several parrot studies (Auersperg et al., 2014; Heyes & Saggerson, 2002; Moore, 1992; Pepperberg, 2006), it may be surprising that the present study failed to find evidence of imitation. Although it is possible that OWAs lack the capacity for motor imitation, I suggest that these results are more likely explained by the experimental design used. The two-action task I used may have been too easy, allowing birds to mainly rely on individual learning to acquire the task. Tennie et al. (2006) identified this as potential explanation for failure to find imitation in great apes in a push-pull task. Furthermore, disparities in findings between field and laboratory research with kea parrots indicate that social learning capacities detected in highly controlled testing, may not be observed under more naturalistic conditions (Gajdon, Fijn, & Huber, 2004; Huber et al., 2001). Across animal species, imitation has been most commonly observed in highly controlled dyadic experiments. Under such testing conditions, there is little to distract an observer's attention from the demonstrator and testing apparatus, and crucially, there is no social competition when the observer is given access to the apparatus. In contrast, as this study's subjects were tested in their aviaries, with all group members being given simultaneous access to the foraging box, several factors may have influenced what subjects ultimately learned about the foraging task. First, it

is much more likely in an open diffusion set-up that subjects obtain less consistent information about the method used by demonstrators to obtain food. Subjects in my study were exposed to alternate task solutions as a result of group members' task acquisition through individual learning. It is also difficult to know what aspects of each demonstration each subject could observe from their position in the aviary. Subjects also had many more competing stimuli to attend to, including a range of social interactions. Second, social competition for access to the foraging box meant that subjects had limited time to interact with the box before being displaced or receiving aggression. This may have encouraged the rapid use of multiple strategies to gain access to the box, rather than careful copying of the demonstrator's technique. Equally, the positive relationship I found between observers displaying aggression to others and successfully opening the box suggests that the most successful birds directed a great deal of their attention towards individuals that came in close proximity to the apparatus. They may therefore have been more interested in displacing group members in the TZ, including the TD, than in observing the TD's manipulation of the box door. All these factors could also be present and constrain the types of social learning that influence the transmission of group-specific behaviours in the wild, so using open diffusion designs in experimental work is vital in order to better understand the social learning mechanisms underlying these cultural variants in animals.

The analyses I conducted concerning the effect of aggression and pilfering on subjects' performance indicate that individual characteristics also influence the likelihood of an individual acquiring a novel foraging technique from others. The positive relationship I found between observers displaying aggression to others and successfully opening the box indicates that willingness to defend access to the resource from others is important in a highly competitive social situation in terms of ensuring

sufficient exploration opportunity to acquire the task solution. Equally, birds who successfully pilfered food from others who opened the box also had high levels of their own successful foraging attempts with the box. Pilfering may be an important scaffolding behaviour in the acquisition of novel foraging techniques. However, this relationship could also be a product of aggressive birds defending an area close to the box door, providing them with a lot of opportunities to open it themselves and pilfer from others. Related to pilfering behaviour, I also anecdotally observed that some individuals in the present study spent more time scrounging for dropped food rewards on the ground below the TZ, than they did attempting to open the box themselves. Thus, for some subjects, benefiting from group members' successful manipulation of the box may have had an inhibitory effect on their task acquisition, as was seen in Giraldeau and Lefebvre's (1987) pigeon study. Unfortunately, because this behaviour occurred outside the TZ, it was not captured on video and could not be systematically examined. Contrary to our predictions, receiving aggression or having food stolen did not appear to deter subjects' efforts to interact with the box. However, it could be that only the more socially confident birds that were relatively resilient to aggression and pilfering chose to regularly enter the TZ to interact with the box. The use of multiple foraging boxes in future studies may reduce aggression and social competition, possibly yielding different results.

In conclusion, the present study found evidence of social learning through locale/stimulus enhancement or emulation. In this open diffusion set up experimental birds who could watch a trained demonstrator were more likely than control birds to approach the box and successfully extract food from it; however, I found no evidence that they imitated the method used to open the box. Aggression was relatively frequent as individuals competed to gain access to the monopolisable food source. Surprisingly,

subjects were not deterred from making physical contact with the box as a result of receiving aggression from or having food stolen by group members; however, subjects that frequently displayed aggression towards others and pilfered food from others also had high levels of successful box opens. This indicates that propensity for aggression may play a role in the extent to which birds are able to capitalise on opportunities to learn about, and compete for, monopolisable food that requires extractive foraging techniques to be developed. This study shows that imitation is not necessary for the spread of exploitation of a novel food source when relatively basic extractive behaviours are required. While some species may show greater reliance on high fidelity copying (e.g., great tits; Aplin et al., 2015), which would allow adaptive behaviour to spread more rapidly through populations, others may rely more heavily on individual learning and thus may show greater propensity for innovative behaviour. A trade-off may therefore exist between innovative behaviour and social learning. My open diffusion study highlights important social and individual factors that constrain and promote learning from others in a naturalistic context, as well as the possibility that although tightly controlled dyadic social learning paradigms have shown many animals to be capable of imitation, group-specific behavioural variations observed in the wild could result from lower-fidelity copying processes.

The following chapter includes further exploration of factors that may be associated with performance on the two action task. In addition to comparing performance on the two action task between OWAs and BGMs (Study 2), a correlational analysis is reported (Study 3) that assesses the potential relationship between OWA and BGM task acquisition and scores on relationship quality measures (obtained in the observational study reported in Chapter 4). First, however, a study on cooperative problem solving is reported (Study 1). Like social learning, cooperative

problem solving appears to be widespread across a range of species, involving capacities that range from simple to complex.

CHAPTER 7: SOCIAL COGNITION

Abstract

Cooperation and the social transmission of behaviour have been reported in a variety of avian species, including in wild and captive populations. However, the extent to which these behaviours are explained by complex cognitive processes remains unclear. The studies reported in this chapter investigate OWA and BGM performance on a cooperative ('loose string') and a social learning (two-action, open diffusion) task (Study 1 and 2, respectively). Within species analyses of potential covariates (affiliative investment and boldness) are reported in Study 3. Both species performed poorly overall in the loose string familiarization phase; most birds in each group failed to meet criterion and were unable to move onto the test phase. BGMs that met criterion could not be tested because they exhibited extremely low levels of social tolerance. One OWA dyad completed the loose string task, showing evidence of the capacity to synchronize behaviour to solve the task (as measured by their performance on simple cooperative tests), but showed no evidence of having an understanding of the roles their partners played in attaining the solution (as measure by performance on delayed partner trials). BGMs, like OWAs, showed evidence of task acquisition in the social learning experiment (all findings for the OWA social learning study are reported in Chapter 6, and summarized in this chapter); no significant between species differences were found in their performance. Social learning task performance and levels of affiliative investment (as measured by composite preferred partner scores) were found to be positively correlated in BGMs, but not OWAs. Evidence was also found that individual variation in boldness was associated with social learning task acquisition in BGMs.

Introduction

Behaviours that appear to involve complex social cognitive processes have widely been documented in social species. Cooperative behaviour, for instance, has been observed in primates, birds, cetaceans, and social carnivores, occurring in a variety of contexts in the wild (e.g., hunting, breeding, resource competition, and predatory defence; Cheney, Moscovice, Heesen, Mundry, & Seyfarth, 2010; Foster, 1985; Langergraber, Mitani, & Vigilant, 2007; Ligon, 1983; Möller, Beheregaray, Harcourt, & Krützen, 2001; Packer & Pusey, 1997; Sachs, Mueller, Wilcox, & Bull, 2004). These observations raise important questions about the degree of understanding animals have about the roles they and their partners play in cooperative interactions. Similarly, the common occurrence of group-specific behaviour among wild animals has fuelled debates about the extent to which animal ‘traditions’ rely on social learning processes (Laland & Hoppitt 2003). Addressing these issues through extensive comparative research is of tremendous value as doing so informs our understanding of the evolutionary origins of human cooperation and culture. It is not only important to identify species’ social cognitive capacities, but to also identify how other factors (e.g., variation in individual traits) may influence or be related to problem solving within the social domain.

In this chapter, I present three studies conducted on OWAs and BGMs. In the first, subjects are assessed, and species compared, on performance on a cooperative task. In the second, species are compared on a social learning task, and in the last study, subject task performance is related to the amount of affiliative investment subjects demonstrated in their relationships with preferred partners (both species), as is boldness (BGMs only).

Study 1: Measuring cooperative problem solving in using a loose string task

Introduction. As the scope of cooperative behaviour in the animal kingdom is highly varied, different definitions of cooperation have been offered by researchers. While some regard cooperation as a feature of long-term partnerships, in which behaviours such as reciprocity and mutualism are expressed over a prolonged period of time (Mendres & de Waal, 2000), others define it more narrowly. According to Noë (2006), cooperation takes place when individuals' joint actions produce "immediate benefit for all participants involved" (p. 2). It is the latter form of cooperation that is the focus of this study.

Despite the widespread documentation of animal cooperation, significant questions remain about the mechanisms that underlie it. The greater the apparent behavioural complexity of a cooperative event, the more consideration is generally given to the involvement of cognitive mechanisms (as opposed to genetic pre-programming or conditioned responses); for instance, 'acting apart together' (simultaneously engaging in similar actions towards the same target without coordinating those actions) has been identified as a basic form of cooperation, as a desired outcome can be achieved without participants having an understanding of the roles they and their partners played in achieving that outcome (Noë, 2006). In contrast, cooperation that involves coordination of complimentary actions, or collaboration such as through communication, has been argued to provide evidence of the involvement of more complex cognition (Boesch & Boesch, 1989; Noë, 2006). As is the case with other seemingly complex behaviours, gaining a true understanding the role of cognition in animal cooperation requires experimental investigation.

Originally developed to study cooperation in primates (Halsey, Bezerra, & Souto, 2006; Hirata, 2003; Melis, Hare, & Tomasello, 2006) the 'loose string' task has

become one of the most valuable tools for researchers that want to measure species' capacity to synchronize and coordinate behaviour with social partners. In this task, a baited tray is placed out of subjects' immediate reach; a single string is threaded through rings attached to two corners of the tray, and string ends are made available to subjects. To pull the tray within reach (usually sliding it through a gap in a door or cage), each member of an experimental dyad must grasp and pull on a string end. Partners must act in unison, as pulling without the aid of a partner causes the string to become unthreaded, thus making it impossible to retrieve the tray. In the simple version of this test, each experimental partner is positioned facing a string end and both are given simultaneous access to string ends. This allows researchers to test subjects' capacity to act in synchrony with a partner to solve a problem. However, as previously indicated, there is a limit to what can be concluded about subjects' understanding of the task based solely on observed behavioural synchrony. To address this, researchers vary the temporal or spatial distribution of experimental partners. For example, in the 'delayed partner' condition, one partner is first given access to the testing apparatus, and after a delay of several seconds, the second partner is allowed access. A subject's ability to wait for a partner's arrival, and then initiate the appropriate response in unison with that partner, has been argued to be indicative of an appreciation of the essential role a partner plays in solving the problem (Melis et al., 2006; Plotnik, Lair, Suphachoksahakun, & de Waal, 2011; Seed, Clayton, & Emery, 2008).

One of the most valuable aspects of the loose string paradigm is that it can be adapted to study a variety of species. It has therefore become a standardized way to measure animals' cooperative problem solving abilities, allowing for comparative assessments of species' capacities. Loose string tasks, or variations of the paradigm, have thus far been used to test cooperative problem solving in primates, elephants,

hyenas, dogs and birds (Cronin, Kurian, & Snowdon, 2005; Hirata & Fuwa, 2007; Massen, Ritter, & Bugnyar, 2015; Melis et al., 2006; Mendres & de Waal, 2000; Ostojić & Clayton, 2014; Péron, Rat-Fischer, Lalot, Nagle, & Bovet, 2011; Plotnik et al., 2011; Scheid & Noë, 2010; Seed et al., 2008). From a comparative perspective, one of the most interesting findings that have emerged from this research is the disparity between avian and mammalian performance on loose string task conditions that test subjects' understanding of the role played by cooperative partners in solving the task. Social mammals (listed above) have shown the capacity to delay responses until partners arrive, and/or appropriately select between a 'solo' tray (can be operated by one individual) and a 'duo' tray (requires the cooperative effort of a dyad), depending on whether they are being tested alone or with a partner (Cronin et al., 2005; Drea & Carter, 2009; Melis et al., 2006; Mendres & de Waal, 2000; Ostojić & Clayton, 2014; Plotnik et al., 2011). In contrast, performance was poor when ravens, rooks, and African grey parrots were tested on these conditions; yet, in the simple cooperative test condition, when birds were given simultaneous access to string ends, corvids and parrots performed similarly well (Massen et al., 2015; Péron et al., 2011; Seed et al., 2008).

The poor performance of corvids and parrots in the more difficult conditions of the loose string task is surprising, not only because of the cognitive similarities that have been found between these birds and primates (see Chapter 1 for a discussion of primate and bird similarities), but also because of the complex cooperative partnerships corvids and parrots naturally form (see Chapter 1 for a discussion of corvid and parrot similarities). They engage in bi-parental care, rearing altricial young that have long developmental periods (see Chapter 4 for a discussion of cooperative partnerships found in corvids and parrots). In this context, the capacity to effectively cooperate and

coordinate behaviour is highly adaptive, as evidenced by captive studies that have shown significant positive correlations between these variables and breeding success (Spoon, Millam, & Owings, 2006, 2007).

It has been suggested that the disparity between primate and corvid performance in the more challenging cooperative conditions may be explained by differences in socio-ecology (Massen et al., 2015; Seed et al., 2008); while both develop stable partnerships, fission fusion dynamics characterize primate societies, whereas corvids, like parrots, primarily interact with their mates and kin (Amici, Aureli, & Call, 2008; Forshaw, 2006; Hoppe, 1992; Seibert, 2006; Spoon, 2006; Symington, 1990; van Schaik, 1999). However, as findings from only three avian species have been published using the loose string paradigm, these explanations may be premature; more research is needed before conclusions can be reached regarding similarities and differences between primates and corvids or parrots in their understanding of the task. It is therefore necessary to expand our use of this testing paradigm with additional species. The study I report in this chapter, which investigated and compared OWA and BGM performance on the loose string task, contributes to this effort.

The OWA and BGM cooperative problem solving experiment I conducted followed procedures used in the rook (Seed et al., 2008) and African grey (Péron et al., 2011) studies. OWAs and BGMs were first individually familiarized with the loose string task. After meeting criterion in the familiarization phase, dyads were given the simple cooperation test and the delayed partner arrival test. I used the familiarization procedures used by Seed et al., as they were more rigorous than those used by Péron et al. While the African greys were considered to have met training criterion when “all birds were able to stay in front of the cage and pulled on the string” with the help of a human partner (Péron et al., 2011, p. 547), Seed et al. individually trained their

subjects, and required the rooks to pass three familiarization conditions that got progressively more difficult before they could move on to test trials. The familiarization procedures used by Seed et al. ensured that subjects learned that both strings needed to be pulled to gain access to the food.

The research aims of Study 1 included investigating whether OWAs and BGMs show evidence of being able to synchronize behaviour with social partners to solve the loose string task, and whether they show evidence of understanding the need and role of their partner in successfully completing the task (measured through delayed partner arrival tests). Lastly, I aimed to investigate potential between species differences in task performance. Based on performance observed in corvids and the African greys (Massen et al., 2015; Péron et al., 2011; Seed et al., 2008), OWAs and BGMs were expected to pass familiarization trials and show better performance on the simple cooperative test than the delayed partner arrival test. No prediction was made concerning whether interspecies differences would be found.

Methods.

Research site. This research was conducted at Lincolnshire Wildlife Park (see Chapter 4 for details).

Subjects. Twelve OWAs (four females, eight males) and six BGMs (two females, four males) were tested on the loose string task. All subjects were believed to be adults. Each species was group-housed in its own aviary. Further information concerning identification, housing, and diet can be found in Chapter 4.

Training/testing compartments. Subject aviaries contained compartments in which subjects were trained and tested (see general methods in Study 1, Chapter 5 for details).

Data collection period. For both species, training and data collection took place between the months of October and November in 2012 (OWAs) and 2013 (BGMs).

Materials and experimental set up. Flat rectangular trays were used to test both species (see Figure 7.1). OWAs were tested using a cardboard tray (25 x 10 cm) and BGMs were tested using a wooden tray (22 x 10 cm). Both trays contained two plastic loops made from zip ties, through which a piece of string was threaded (see Figure 7.1). A plastic circular dish, which was baited during test trials, was attached to the OWA tray. The BGM tray originally contained the same dish; however, as BGMs repeatedly tore it off during habituation, it was not used during training trials. Instead, a strand of rope was glued around the inner edges of the tray to prevent food rewards from rolling off during trials (see Figure 7.1).

Trays were placed inside a testing cage, behind a transparent plexiglass panel. There was a 4.5 cm gap between the bottom of the plexiglass and the table, through which string ends extended (7 cm) and the tray could be pulled (see Figure 7.1). The tray could only be pulled through the gap by pulling on both string ends simultaneously; pulling on one would result in the string becoming unthreaded. Panels (cardboard for OWAs, 50 x 28 cm; plastic for BGMs, 42 x 30 cm) were used to block subjects' visual and physical access to the experimental set up between trials.



Figure 7.1. Photos of the experimental set up (a) and trays used for OWA (a) and BGM (b) loose string task trials.

Procedure.

Pre-training. OWAs and BGMs were habituated to myself and all experimental materials prior to data collection. Birds were trained to enter training/testing compartments and to approach experimental materials using operant conditioning techniques (see Study 1 general methods in Chapter 5 for details). All subjects were trained to pull strings to obtain rewards prior to the commencement of this study, as they had previously completed the horizontal string pulling task (see Experiment 3, Study 1 in Chapter 5 for details).

Experimental session frequency and duration. One to two experimental session(s) was (were) held per day, each lasting between 1.5 and 2 hrs. Sessions took place between morning and afternoon feeds. Each subject was allowed to complete up to 20 trials per day (10 trials per session).

Familiarization. Following the procedure used by Seed et al. (2008), OWAs and BGMs were individually familiarized with the loose string task. In order to ensure subjects recognized that both strings needed to be pulled in order for the food to come within reach (Seed et al., 2008), they were required to pass three levels of training that got progressively more difficult before moving onto testing. At the first level, string ends were overlapping; in the second, they were positioned 1 cm apart, and in the third,

they were 6 cm apart. In the overlapping and 1 cm apart conditions, it was possible for subjects to pick up both string ends in one action. In the third condition, subjects had to pick up one end, hold it with their beaks or with a foot, and then pick up the other end before pulling. Responses were considered correct if subjects grasped both string ends and pulled the tray through the cage gap. They were considered incorrect if subjects pulled on one string end and the other end either became unthreaded or was pulled so far into the cage that it was no longer possible to use it to pull the tray out. Incomplete trials, in which subjects began to pull on the string, but did not complete the motion (they were given up to 3 min to do so), were repeated. In order for subjects to move from one condition to the next, they were required to correctly respond on three consecutive trials. If subjects had incorrect responses on three consecutive trials, they returned to the previous condition, having to once again meet criterion in that condition. In order for subjects to move into the cooperative testing phase, they were required to respond correctly on three consecutive trials in the 6 cm condition. Subjects were given up to 120 trials to meet criterion in familiarization trials.

Simple cooperation test. The simple cooperation task procedure I used was based on procedures that were used by Péron et al. (2011) and Seed et al. (2008). Dyads were created that were composed of individuals that met criterion in the familiarization phase. Dyad partners were tested together using the same materials and set up as was used in the familiarization phase. However, string ends were positioned so that a single individual would be unable to bring both ends together and pull the tray (25 cm apart, extending 7 cm outside the cage). Trials began when both partners were positioned in front of the testing cage, facing it; dyad partners were thus given simultaneous access to string ends. Responses were considered correct if each partner grasped a string end and simultaneously pulled the tray through the cage gap.

Responses were considered incorrect if only one partner pulled on the string. Subjects that met criterion in this test (9 correct responses in 10 consecutive trials) were given the delayed partner test. Birds were given up to 120 trials to meet criterion

Delayed partner arrival test cooperation test. The procedure I used for the delayed partner arrival test was also based on procedures used by Péron et al. (2011) and Seed et al. (2008). The testing tray and string ends were set up as they were in the simple cooperation test. However, in this test one dyad partner was the experimental bird and the other was considered the cooperative partner. Prior to a trial commencing, a testing panel was used to move both birds to the end of the table so that they were positioned opposite the testing cage and tray; the panel was placed directly in front of the birds, between them and the testing apparatus, blocking them from access to the tray's string ends. Test trials began when the panel was slid and the experimental bird was allowed to walk across the table to the testing apparatus. The cooperative partner was kept behind the panel for 10 s before also being given access to string ends. Experimental bird responses were considered correct if they were able to delay pulling on the string until their partner arrived and also pulled on the string. Dyad partner roles were counterbalanced in each session, with both individuals serving as the experimental bird in 5 trials and the cooperative partner in 5 trials. Birds completed a total of 20 trials in each role.

Data analysis. The number of OWAs and BGMs that passed each familiarization condition were calculated, as were the number of trials it took for birds to pass each familiarization condition, and the number of trials it took birds to meet criterion in the simple cooperation test. Experimental birds' correct and incorrect responses on the delayed partner test were also calculated. Nonparametric tests were used due to small sample sizes. A Fisher's exact test was run in order to determine

whether there were interspecies differences in the proportions of OWAs and BGMs that passed each condition. Mann Whitney tests were run to compare OWAs and BGMs on the number of trials it took subjects to pass each condition.

Results.

Familiarization trials. Of the 12 OWAs that began the familiarization phase of the loose string task, four did not complete it; one subject was removed from the aviary to undergo veterinary care and the other three stopped coming into the testing compartment to complete trials. All six BGMs completed the familiarization phase (meeting criterion or completing 120 trials). The numbers of OWAs and BGMs that met criterion in each familiarization condition can be seen in Table 7.1. Fisher's exact tests showed that there were no significant differences in the proportions of OWAs and BGMs that passed conditions 2 (OWA, 7/8; BGM, 6/6, $p = 1$) and 3 (OWA, 3/8; BGM, 3/6), $p = 1$. Mann Whitney tests showed that OWAs required significantly more trials to pass conditions 1 (OWA, $N = 8$, $Mdn = 15$, $IQR = 14$; BGM, $N = 6$, $Mdn = 6.5$, $IQR = 3$; $U = 4.5$, $z = -2.36$, $p = .018$, $r = -.65$) and 2 (OWA, $N = 7$, $Mdn = 24$, $IQR = 28$; BGM, $N = 6$, $Mdn = 11$, $IQR = 7$; $U = 2.5$, $z = -2.65$, $p = .008$, $r = -.73$) than BGMs. Too few birds passed condition three to compare their performance with inferential statistics, but descriptively, OWAs needed more trials ($Mdn = 113$) than BGMs ($Mdn = 82$).

Table 7.1

Numbers of OWAs ($N = 8$) and BGMs ($N = 6$) that met criterion in familiarization conditions 1 (overlapping), 2 (1 cm apart), and 3 (6 cm apart)

Species	Condition 1	Condition 2	Condition 3
OWA	8	7	3
BGM	6	6	3

Simple cooperation test. As three OWAs and three BGMs passed the familiarization phase, leaving one OWA and one BGM without partners for cooperative tests, the decision was made to include an OWA and a BGM that had failed to meet criterion, but had come close to it (responding correctly on two consecutive condition 3 trials). Although two OWA and two BGM dyads began the simple cooperation test, only one OWA dyad completed it. BGMs testing had to be terminated due to the lack of social tolerance individuals showed towards each other; the frequency of agonistic interactions dyads displayed when they were positioned in front of the testing apparatus made it impossible to test them. As this could not be remedied, the study was discontinued with this group. One OWA dyad did not complete the simple cooperation test because, after two sessions, one of the partners stopped coming into the testing compartment, showing no interest in completing the task. Out of the 20 trials that dyad completed, they successfully pulled the tray and obtained food in six of them (all correct responses were in the second session). One OWA dyad met criterion in this test, doing so in 51 trials (6 sessions, two were incomplete).

Delayed partner arrival cooperation test. The OWA dyad that met criterion in the simple cooperation test completed a total of four delayed partner arrival test sessions, with each individual completing a total of 20 trials as the experimental bird and 20 trials as the cooperative partner. Both OWAs failed all trials they completed.

Discussion of Study 1. The overall poor performance of OWAs and BGMs on the loose string task was, for the most part, unexpected. Particularly surprising was the difficulty OWAs and BGMs showed in acquiring the task in the familiarization phase. While all eight rooks tested by Seed et al. (2008) were able to pass the most difficult condition (string ends 6 cm apart), in my study, approximately half of subjects failed to

meet criterion. This difference in performance may be due to morphological differences of their beaks (straight versus curved) or feet (three toes facing forward and one backward versus two forward and two backward). The motor coordination required to grasp one string end, hold it while retrieving the second one, and then simultaneously pull on both, may have been more challenging for parrots due to these anatomical differences. Unfortunately, as no other parrot species have been exposed to the loose task familiarization procedure developed by Seed et al. (2008), it is very difficult to determine whether this is a plausible explanation.

The overall poor performance of OWAs and BGMs in this task was similar to their performance in the string-pulling discrimination phase of the means-end experiment that is reported in Study 1, Chapter 5 (2/12 OWAs and 0/9 BGMs met criterion). As suggested in the study's discussion and in the chapter's general discussion, factors associated with visual perception may have interfered with birds' ability to attend to key aspects of the task (e.g., white strings against a grey background provided little contrast, and artificial light was used, which may not have provided full spectrum light or may have emitted noncontinuous light). An additional limitation of procedures used in the loose string task, is that OWAs and BGMs were given immediate access to strings at the start of trials. This may allowed them to respond impulsively, without focusing on task features. This could be addressed in future studies by incorporating an observation period (see the general discussion of Chapter 5 for further details).

Although the three-condition familiarization procedure was used to ensure subjects' recognition of the need to pull on both string ends to obtain access to the tray, this approach may not be appropriate for parrots and could also explain the poor performance that was observed. The approach taken by Péron et al. (2011) serves as an

alternative; African greys were first given access to the tray with the string ends attached to it so that it could be pulled by one individual. In the second and last condition of the familiarization phase, the string was loose and birds were required to pull on one end, while an experimenter pulled on the other. Although the rooks tested by Seed et al. (2008), which were exposed to the more rigorous familiarization conditions, appear to have shown faster acquisition of the basic cooperative test than the African greys in Péron et al.'s (2011) study, the performance of these two species on the delayed partner arrival and apparatus choice tests were similar. A rigorous familiarization procedure may therefore be unnecessary, and may ultimately be more of a test of motor coordination than task understanding.

Poor performance in the familiarization phase meant that only two dyads in each species were given cooperative tests. Unfortunately, only one dyad (OWAs) completed testing. The second OWA dyad completed simple cooperative test trials, but one partner stopped coming into the testing compartment before data collection on this test was completed; motivation was therefore likely a factor in OWA performance. This conclusion is further supported by the fact that three OWAs that began familiarization trials failed to complete this experimental phase. It should be noted that data collection for the loose string task occurred in the fall season (for both species). This is potentially significant, as during this time, birds were being given higher quantities of food as part of their regular feed than they had been given in previous months. This was done to increase body fat content to prepare birds for winter months. The increase in food quantity may thus have decreased subject motivation to participate in trials in order to obtain food rewards.

The OWA dyad that completed the simple cooperation test met criterion, and therefore showed the capacity to synchronize behaviour to cooperatively solve the

loose string task. This was not surprising, not only because it is consistent with previous avian research (Massen et al., 2015; Péron et al., 2011; Seed et al., 2008), but also because of the synchronous/coordinated behaviour documented in the OWA relationship quality observational study I conducted (presented in Chapter 4). In the delayed partner arrival condition, the two OWAs showed no capacity to inhibit the response of pulling on the string until their partner's arrival. This poor performance is similar to what has been observed in previous avian studies. In separate studies, ravens and rooks showed successful cooperation in approximately 2% of delayed partner arrival trials (Massen et al., 2015; Seed et al., 2008). In Péron et al.'s (2011) study, two of three African greys showed no ability to delay string pulling and one showed evidence of improvement across trials (demonstrating higher latency to approach strings). In all three of these studies, the authors concluded that while subjects were able to synchronize their behaviour with partners to solve the loose string task, they showed little or no evidence that they had an appreciation for their partners' roles in the task. As only one OWA dyad completed this test, little can be concluded about OWAs' capacity to understand the role played by cooperative partners in the loose string task.

In contrast to OWAs, BGMs showed little to no social tolerance in the dyadic testing condition, and due to frequent and intense aggression between partners, they could not be tested. This is consistent with findings from a between species analysis presented in Chapter 4 showing that social tolerance composite scores (measuring level of aggression and approach tolerance displayed by focal birds towards their preferred partners) were significantly higher in OWAs than BGMs. In corvid studies, researchers report associations between social tolerance measures (e.g., willingness to feed from the same dish as a partner) and performance on cooperative tests (Massen et al., 2015; Seed et al., 2008). Similarly, Péron et al. (2011) report that African greys showed

evidence of social preference, demonstrating greater willingness to engage in the cooperative task depending on which individual they were tested with. These findings suggest that consideration must be given to dyadic partner composition, and the potential role social tolerance and/or partner preference may play in avian performance on loose string tests (discussed further in Study 3 of this chapter).

Although little can be concluded about OWAs' and BGMs' understanding of the loose string task based on the results obtained through this study, this study provides valuable information about the methodological challenges that may be experienced when testing parrots using the loose string paradigm. It is suggested that future psittacine researchers carefully consider whether performance may be impacted by species' morphology or motor coordination capacities. Furthermore, assessing factors such as food motivation and social tolerance can be highly valuable, as these factors also likely impact on task performance.

Study 2: Social Learning in OWAs and BGMs

Introduction. As discussed in detail in Chapter 6, social learning processes are highly valuable, as they allow for the rapid transmission of efficient behaviour. Several forms of social learning have been identified; high fidelity copying, for example, is considered to be complex compared to stimulus enhancement or emulation (Caldwell & Whiten 2002). For those wishing to better understand the evolution of culture, identifying interspecies variations in social learning capacities is essential.

The present study focuses on comparing OWA and BGM performance on a social learning task, in which their capacity to acquire novel foraging behaviour was tested using a two-action box and an open diffusion design (see Chapter 6 for descriptions of paradigms and discussions of their benefits). Subjects in both groups

were exposed to trained demonstrators using a slide action to open the testing apparatus (pull was the alternate action that could be used). Research procedures and data collected in the OWA social learning experiment presented in Chapter 6 are summarized in this study, and the social learning experiment conducted on BGMs is presented.

Unfortunately, only one BGM group was available for study. As no comparisons could be made between experimental groups and control groups for BGMs, it was not possible to draw conclusions about the forms of social learning that were likely involved in their performance (the OWA study presented in Chapter 6 provides comparisons of experimental and control groups). As such, the objectives of this study were focused on engaging in between species analyses, which included comparing the proportions of OWAs and BGMs that: (1) approached the box (entered the TZ), and (2) successfully opened the two-action box. The methods subjects used to open the box (slide or pull) were also compared. Due to the lack of psittacine research that examines between species differences in social learning tests, no prediction was made about whether OWAs and BGMs would differ significantly in their performance. Levels of aggression OWAs and BGMs displayed were also assessed. High levels of agonistic behaviours were expected (for both groups) due to the socially competitive environment that was created by using the open diffusion design. As BGMs (but not OWAs) had shown extremely poor social tolerance in simple cooperative test trials (resulting in the discontinuation of the study; see Study 1 of this chapter), I compared frequencies of agonistic behaviour in the two groups to determine whether BGMs once again demonstrated relatively low levels of social tolerance.

Methods.

Research site. This research was conducted at Lincolnshire Wildlife Park (see Chapter 4 for details).

Data collection period. Data on the OWA group was collected in July 2012. BGM data was collected in September 2013.

Subjects. Study groups consisted of 23 OWAs (9 females and 14 males) and 12 BGMs (8 males and 4 females). Each species was group-housed in its own aviary. Further information concerning housing, identification, and diet can be found in Chapter 4.

Pre-training. OWAs and BGMs were habituated to the experimenter (see Chapter 4 for details) and were trained to enter testing compartments located within their aviaries (see Chapter 5 for details). One demonstrator in each experimental group who showed high levels of food motivation, social tolerance, willingness to remain in the training compartment and low levels of neophobia was selected (see Chapter 6 for details). During the two weeks that preceded test trials, study groups were habituated to three cameras mounted on tripods, positioned as they would be during experimental trials (see Figure 6.2 in Chapter 6).

Experimental box. Two-action wooden boxes were used to test OWAs and BGMs; boxes contained doors that could be opened by pulling or sliding them. A description and photos (Figure 6.1) of the OWA box can be found in Chapter 6. The BGM box (30 x 11.5 x 24 cm) was covered in a thick layer of aluminium to protect it from damage that could be inflicted by their powerful beaks (see Figure 7.2); the back had an opening (10 x 10 cm) through which food could be inserted. The box door and its handle measured 14 x 13 cm and 4 x 1.5 x 2.5 cm, respectively. OWA and BGM demonstrators were exposed to the same experimental box set up during training (see Chapter 6 for details). Study groups were exposed to the same testing set up; an area in

each aviary was identified as the ‘target zone’ (TZ); the box was placed in the centre of the TZ, and a perch (OWA = 43.8 x 23.5 cm; BGM = 47 x 26 cm) was mounted underneath the box; three cameras were used to video subject activity in the TZ during test trials. A detailed description of the testing set up, including illustrations of the set up (Figure 6.2) can be found in Chapter 6.



Figure 7.2. Photo of the experimental box used in BGM test trials.

Demonstrator training. OWA and BGM demonstrators were both trained to open the box using the slide action, and were trained using the same procedure (see Chapter 6 for a description).

Testing procedure. Study groups were exposed to the same testing procedure; the box was mounted and baited inside the aviary TZ; one experimenter provided real time commentary of behaviour in the TZ onto the video recordings, and a second experimenter re-set and re-baited the box; 24 pieces of food were available in each trial. Criteria used for determining the end of trials can be found in Chapter 6, along with a more detailed description of testing procedure. OWAs completed 9 trials and BGMs completed 10; BGMs were given an extra trial as one of their test trials was ended prematurely due to one subject’s aggression towards group members and destructive behaviour towards the experimental box.

Video Coding. The coding scheme and rules used to code videoed subject behaviour can be found in Table 6.1 in Chapter 6. All behaviours listed in Table 6.1 were coded for OWAs, using the Observer XT 10 program. The following behaviours were coded for BGMs: box approaches ('inside TZ'), successful box opens (including 'opens successfully' and 'fully successful'), and agonistic behaviours subjects exhibited towards others in the TZ ('unidirectional agonistic'). BGM behaviour was coded manually using Windows Media Player.

Data analyses. The number of successful box opens completed by demonstrators and subjects were calculated, as were the number of subjects that entered the TZ in each group. Total frequencies of unidirectional agonistic behaviour were also calculated. Due to small sample sizes, nonparametric tests were used for within (two-tailed Wilcoxon signed rank) and between (Fisher's exact and Mann Whitney) species comparisons. In order to determine whether subjects were more likely to use the demonstrated method to open the box than the non-demonstrated method, the number of opens using each method was compared. OWA and BGM study groups were compared to determine whether there were significant between species differences in the proportions of subjects that entered the TZ, opened the box, or demonstrated aggression. A between species analysis was also run comparing total frequencies of unidirectional aggression. Descriptive statistics are presented in cases where N is less than 6 and non-parametric inferential statistics are unable to return a significant result.

Results.

OWAs: Summary of data presented in Chapter 6. The OWA demonstrator successfully opened the box a total of 82 times (11 in Trial 1 and 15 in Trial 2), demonstrating the slide method in 80 opens. Out of 22 OWA subjects, 20 entered the TZ, and seven successfully opened the box, with subjects opening it a total of 121 times

(71 % using the pull method; see Table 7.2). A two-tailed Wilcoxon signed-rank test showed that OWAs that successfully opened the box ($N=7$) did not use the demonstrated method ($Mdn = 1.00$, $IQR = 8$) significantly more than the non-demonstrated method ($Mdn = 1.00$; $IQR = 30$), $z = -.14$, $p = .892$, $r = -.05$; see Table 7.2. Unidirectional agonistic behaviour was seen in all OWA trials ($N = 175$ agonistic events), with 15 of 23 non-individuals (including the trained demonstrator) displaying unidirectional aggression to another bird at least once in the TZ.

BGMs. The BGM demonstrator opened the box a total of 114 times (11 in Trial 1 and 6 in Trial 2), demonstrating the slide method for all opens. Out of 11 BGM subjects, eight entered the TZ and four opened the box, with subjects opening it a total of 84 times (96% using the pull method; see Table 7.2). Unidirectional agonistic behaviour was seen in 9 of 10 BGM trials ($N = 31$ agonistic events), with 5 of 12 individuals (including the trained demonstrator) displaying unidirectional aggression at least once in the TZ.

Due to intense agonistic displays one subject (Sid) directed towards individuals within or approaching the TZ from trial 2 onwards, which prevented others from interacting with the box, Sid and his partner Gizmo were removed from the aviary (after Trial 3) and reintroduced into the large macaw colony.

Table 7.2

The number of box opens OWA and BGM subjects completed using each method and the total number of opens they completed (using either method).

Species	Subject	Slide	Pull	Total
OWA	Piglet	28	30	58
	Pete	9	43	52
	Willy	1	1	2
	Penny	1	1	2
	Freckles	6	0	6
	Mac	1	0	1
	Rocky	1	0	1
BGM	Psycho	0	40	40
	Sid*	2	1	3
	Oscar	0	26	26
	Digbee	1	14	15

*Removed from aviary after Trial 3

Between species comparisons. Of the total number of successful box opens that were observed (including demonstrators and subjects), 41 % of box opens in the OWA group were done by the demonstrator, and 58% of box opens in the BGM group were done by the demonstrator. Fisher's exact tests showed that the proportions of OWA and BGM subjects that entered the TZ (OWA = 20/22; BGM = 8/11), opened the box (OWA = 7/22; BGM = 4/11), and displayed unidirectional aggression at least once (including trained demonstrators; OWA = 10/23; BGM = 5/12) were not significantly different in the two species (subjects that entered TZ, $p = .304$; subjects that opened the box, $p = 1$; birds that displayed aggression, $p = .736$). A Mann-Whitney test showed that the total number of unidirectional aggressive behaviours OWAs ($N = 23$, $Mdn = 0$, $IQR = 5$) and BGMs ($N = 12$, $Mdn = 0$, $IQR = 3$) exhibited were not significantly different in the two groups ($U = 129.50$, $z = -.33$, $p = .771$, $r = -.06$).

Study 2 Discussion. Although there were twice as many subjects in the OWA group as in the BGM group, performance on the two-action task was found to be

similar in the two species. Both demonstrators performed well, frequently and consistently using the slide method to open the box. Additionally, no significant difference was found between the proportions of OWA and BGM subjects that entered the TZ and successfully opened the box, and both groups used the non-demonstrated method (pull) more frequently than the demonstrated method (slide).

As these species are closely related and have many socio-ecological characteristics in common (see Chapter 3 for a description of study species), it is not surprising to find that they behaved similarly in this task. As OWAs and BGMs are social foragers that rely on food that is temporally and spatially dispersed in the wild, the capacity to attend to, and learn from, conspecific behaviour in the context of foraging is likely very valuable for both species. Although conclusions cannot be drawn about whether stimulus enhancement likely occurred in BGMs, as their performance could not be compared to a control group, results for the OWA experiment reported in Chapter 6 suggest that stimulus enhancement and/or emulation likely played (a) role(s) in experimental group performance. No evidence of imitation was found in either OWA or BGM task performance. However, as discussed in Chapter 6, factors other than social learning capacity may explain this (e.g., the pull action may be a more natural foraging behaviour and the open diffusion design created a competitive social environment that likely affected what individuals attended to).

No significant differences were found in levels of aggression OWAs and BGMs exhibited in the TZ. Anecdotally, however, agonistic behaviours observed in BGMs appeared to be more intense, and included displays that did not appear to have been exhibited by OWAs. Two BGMs, for instance, were observed repeatedly lunging very rapidly and forcefully at other group members (one of them was Sid, who had to be removed from the aviary due to aggression towards non-partners). These individuals

also displayed ruffled feathers and gapped open beaks when others were in the TZ or close to its boundaries. These anecdotal observations indicate that there may be meaningful differences in the types of agonistic behaviours OWAs and BGMs exhibit, which could affect task acquisition in a socially competitive environment.

Study 3: Potential covariate of performance on social cognitive tasks - affiliative investment and boldness

Introduction. As discussed in Chapter 5, investigations of potential correlations between variation in cognitive task performance and variation in individual characteristics (e.g., boldness, investment in social relationships), can help researchers address important questions about the efficacy of cognitive experimental paradigms and the adaptive value of specific traits in different problem-solving contexts (Carere & Locurto, 2011; Guillette, Reddon, Hoeschele, & Sturdy, 2010; Range, Bugnyar, Schlogl, & Kotrschal, 2006). At present, there is a lack of avian research that explores the potential association between individual variation in relationship quality and cognitive performance. The study reported here was aimed at addressing this research gap by comparing OWA and BGM performance on social cognitive tasks (described in Study 1 and 2 of this chapter) to relationship quality scores obtained from the observational study I presented in Chapter 4. Scores BGMs obtained in the boldness experiment (described in Study 2 of Chapter 5) were also assessed in this study to determine whether this trait was associated with performance on social learning tasks.

Psittacine researchers have identified significant positive correlations between the degree of behavioural synchrony and coordination pairs bonds demonstrate and their breeding success, providing evidence of the adaptive value of these behaviours (Spoon et al., 2006, 2007; discussed in detail in Chapter 4). Synchrony and

coordination are key elements of the cooperative breeding relationship as they make it possible for pair bonds to protect nest sites, hatch eggs and rear young (Forshaw, 2006; Renton, 2004; Renton & Salinas-Melgoza, 1999; Shultz & Dunbar, 2010; Spoon et al., 2006). One would therefore expect that the degree of synchrony or coordination an individual showed with its partner would be correlated with their performance on cooperative tasks, particularly if they were tested with their partner. It was my original aim to run a correlational analysis comparing OWA and BGM performance on the loose string task reported in this chapter with (i) synchrony/coordination individual index scores and (ii) composite relationship quality scores (both reported in Chapter 4). There is reason to believe that the two would be positively correlated as traits and/or processes that would allow subjects to cooperatively solve problems are likely similar to traits/processes that may play roles in the degree of affiliative investment an individual shows (e.g., motivation to engage in a social interaction and attentiveness to social signals). However, as only one OWA dyad, and none of the BGMs, completed cooperative testing (see Study 1 of this chapter for details), it was not possible to carry out this analysis.

Like the capacity to cooperatively solve problems, the capacity to acquire novel behaviour through observation likely relies on factors that also influence the quality of the relationships individuals have; for example, being able to attend to conspecific behaviour, being motivated to interact with the social or physical environment, and having the capacity to remember an individual's past actions, are likely valuable in both contexts. One of the research objectives of this study was to explore this potential association by comparing OWA and BGM composite preferred partner affiliation scores to performance in the social learning task they completed (described in Study 2 of this chapter). Due to the lack of previous avian research which examines this

potential relationship, no a priori hypotheses were made. This study also investigated whether variation in boldness could explain variation in social learning task acquisition (BGMs only). As object exploration and boldness are known to be associated in animals (including birds), it was expected that BGMs that showed higher levels of boldness would be more likely to acquire the task (Bergman & Kitchen, 2009; Fox & Millam, 2006; Frost et al., 2007; Meehan & Mench, 2002; Rockwell, Gabriel, & Black, 2012).

Affiliative investment and performance on the social learning task.

Methods. Methods used to collect the OWA and BGM relationship quality data that was used for the analysis reported in this study are described in Chapter 4. Methods used to collect data on the social learning study are summarized in Study 2 of this chapter, and described in detail in Chapter 6. Criterion for subject inclusion in this study was (i) available social data (2 OWAs were excluded) and (ii) present in all social learning task trials (2 BGMs were excluded).

Data analysis.

Creation of composite preferred partner affiliation scores: summary of Chapter 4 data analysis. Individual affiliative behaviour indices were standardized across focal birds and their preferred partners (within species). See Chapter 4 for details on how preferred partners were identified. The standardized behaviour indices were used to create composite preferred partner affiliation indices (calculated by adding: proximity, allopreening and synchrony/coordination indices; BGM composite scores also included courtship feeding). Composite preferred partner scores were used in this study for within species analyses in order to assess potential associations between relationship quality and performance on the social learning task.

Analysis to determine whether affiliative scores and performance on the social learning task were correlated. A two tailed Kendall's tau test was used to determine whether OWA and BGM composite preferred partner affiliation scores were correlated with the number of box opens subjects completed in the social learning task. Relationship quality data was not available for two OWA subjects that opened the box; they were thus excluded from the analysis. The two BGMs removed from the study aviary prior to the end of the social learning study were also excluded from this analysis, as were social learning task demonstrators.

Did successful birds' preferred partners also show task acquisition? For birds that successfully opened the box at least once, the percentage of their preferred partners that entered the TZ was calculated, as was the percentage of their partners that opened the box. As studies have found that the spread of behaviour can be predicted by social networks (e.g., lobtail feeding in humpback whales, Allen, Weinrich, Hoppitt, & Rendell, 2013), this was considered to be relevant to understanding the social transmission of novel behaviour.

Results. Kendall's tau tests showed that BGM composite preferred partner affiliation scores were significantly positively correlated with the number of box opens subjects made ($N = 8$, $\tau = .62$, $p = .045$; see Figure 7.3). No significant relationship was found between these two measures in OWAs ($N = 13$; $\tau = .18$, $p = .440$; see Figure 7.4). For each bird that had successful box opens (including trained demonstrators), the total number of times they opened the box are reported in Table 7.3. The percentage of successful birds' preferred partners that entered the TZ and opened the box can also be seen in Table 7.3 (reported per group).

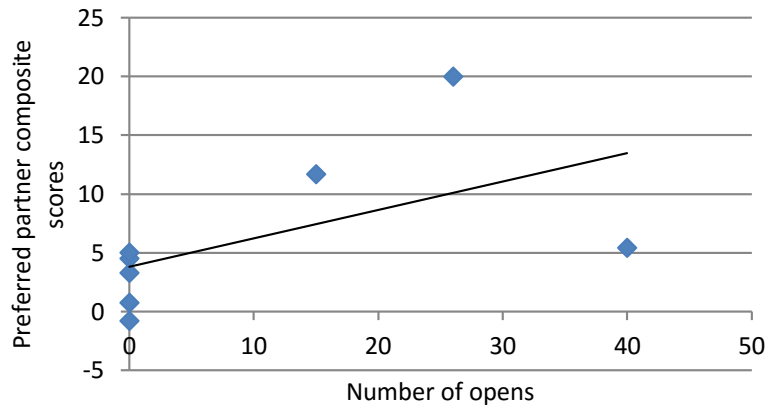


Figure 7.3. Scatterplot illustrating a significant positive correlation between BGM ($N = 8$) box opens and composite preferred partner affiliation scores. Line of best fit is illustrated.

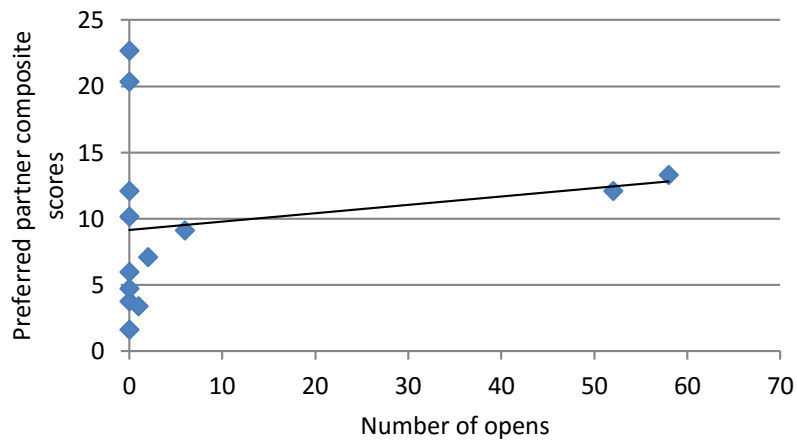


Figure 7.4. Scatterplot illustrating a positive correlation between OWA ($N = 13$) box opens and composite preferred partner affiliation scores. Line of best fit is illustrated.

Table 7.3

Total Number of Opens for Each OWA and BGM that Successfully Opened the Box and the Percentage of their Preferred Partners that Opened the Box at Least Once; Trained Demonstrators are Included (OWA, Benny; BGM, Red)

Species	Bird	Box opens	Percentage of partners that opened box	Percentage of partners that entered TZ
OWA	Benny	82	40%	100%
	Piglet	52		
	Pete	51		
	Freckles	6		
	Penny	2		
BGM	Red	114	80%	100%
	Psycho	40		
	Oscar	26		
	Digbee	15		
	Sid	3		

Boldness and performance on the social learning task.

Method. Methods used to collect BGM boldness data that was used for the analysis reported in this study are described in Chapter 5 (Study 2). Methods used to collect data on the social learning study are summarized in Study 2 of this chapter, and described in detail in Chapter 6. Criterion for subject inclusion in this study was (i) available boldness data (3 BGMs were excluded) (ii) subject in social learning task (1 trained demonstrator excluded) and (iii) present in all social learning trials (2 BGMs were excluded).

Data analysis.

Creation of boldness scores: summary of Chapter 5 data analysis. For each subject, mean latency to obtain food rewards was calculated (across 5 baseline trials). Latencies were also calculated for test trials (5 test objects). Boldness scores were calculated for each test object by subtracting mean baseline latency scores from test

object scores; these scores were then meaned to create boldness scores that were representative of performance across all test trials completed ('overall boldness scores'). The test object with the highest median latency score (across subjects) was identified as the 'highest latency test object.'

Analyses to determine whether boldness scores and performance on the social learning task were correlated. Two tailed Kendall's tau tests were used to determine whether BGM boldness scores ('overall' or 'high latency test object' scores) were correlated with the number of box opens subjects completed in the social learning task or the number of times they approached the box (entered TZ).

Results. Kendall's taus tests showed that BGM ($N = 6$) overall boldness scores were significantly negatively correlated with the number of times subjects opened the box ($\tau = -.89$, $p = .016$; see Figure 7.5). No significant relationships were found between overall boldness scores and number of times subjects entered the TZ ($\tau = -.33$, $p = .348$), highest latency test object scores and number of box opens ($\tau = .01$, $p = 1$), or highest latency test object scores and number of times subjects entered the TZ ($\tau = -.07$, $p = .851$).

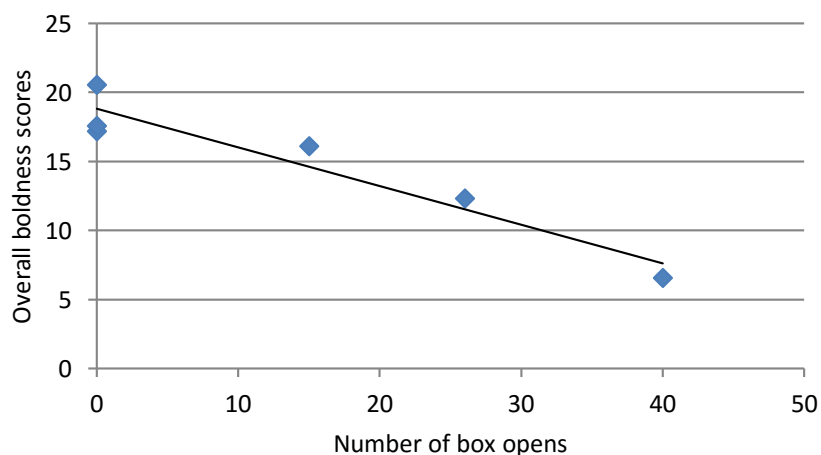


Figure 7.5. Scatterplot illustrating a negative correlation between BGM ($N = 6$) box opens and overall boldness scores. High overall boldness scores indicate high latencies to approach objects, so the boldest individuals have low overall boldness scores.

Discussion of Study 3. Evidence of a meaningful relationship was found between social learning task performance and relationship quality measures in BGMs; BGMs that had higher composite preferred partner affiliation scores were significantly more likely to open the box. This finding is consistent with the idea that factors such as the capacity to attend to social cues and motivation likely play roles in both the ability to obtain information by observing another's behaviour, and the degree to which individuals develop and maintain affiliative relationships. Interestingly, task acquisition and affiliative investment were not found to be associated in OWAs.

The preferred partners of all of the birds that successfully opened the box were found to have approached it on at least one occasion (entering TZ). However, not all partners showed evidence of task acquisition. While preferred partners may have been influenced by others' interactions with the box (stimulus enhancement), they may also have entered into the TZ due to a motivation to maintain close physical proximity with partners that were interacting with the box (see Chapter 4 for a detailed discussion about the role of physical proximity in pair bond maintenance).

Evidence was found that individual variation in boldness was significantly associated with social learning task acquisition. BGMs that had relatively low overall boldness scores (thus showing low latencies to obtain rewards during test trials and high levels of boldness trait) showed greater frequencies of box opens. This finding is consistent with descriptions of bold individuals as showing relatively high levels of object exploration (Bergman & Kitchen, 2009; Fox & Millam, 2007; Frost et al., 2007; Meehan & Mench, 2002; Rockwell et al., 2012). This indicates that in the foraging context, boldness is adaptive, as this trait likely increases an individual's chances of learning how to exploit novel food sources. It should be noted however, that this relationship was not found when box opens were compared to highest latency test

object scores. Additionally, boldness scores were not found to be significantly correlated with the number of times subjects entered the TZ.

General Discussion (Studies 1, 2, and 3)

The similarities that were found between OWA and BGM performance on the cooperative task and social learning tasks, may be explained by their relatively close phylogenetic relationship, and the shared traits that have been found to be predictive of cognitive complexity (e.g., large relative brain size, long life history, and complex socio-ecology; Dunbar & Shultz, 2007; Forshaw, 2006; Iwaniuk et al., 2005; Seibert, 2006; Schweizer et al., 2011; Shultz & Dunbar, 2010). However, these similarities may also be an artefact of the tasks used: the floor effects obtained with the cooperative study design and the lack of control in the open diffusion social learning task mean that further research using different paradigms may reveal species differences in cooperative and social learning capacities. Interspecies or intraspecies variation of non-cognitive factors such as aggression or boldness, and their influence on cognitive performance, must also be considered. As reported in Chapter 6, OWAs that showed higher levels of aggression towards group members were significantly more likely to open the box. Additionally, aggression resulted in the discontinuation of BGM testing in the cooperative task and the social learning task.

The apparent role aggression played in OWA and BGM task performance, coupled with the association that was found between boldness and social learning task acquisition in BGMs, support the notion that non-cognitive intraspecies and/or interspecies variation can often influence subject performance on cognitive tests. This provides another reason why one has to be cautious in the conclusions one comes to based on data retrieved from small samples, or based on comparative assessments of a

particular cognitive capacity that relied on the use of one experimental paradigm (as different traits may be more or less beneficial depending on the problem-solving context).

The significant association that was found between performance on the social learning task and relationship quality scores in BGMs indicates that affiliative tendencies may influence or covary with performance on cognitive tasks. As social cognitive tasks and the maintenance of affiliative relationships involve, and rely on (at least in part), the processing of social information, this correlation makes a great deal of sense. However, this association needs to be further investigated, as avian research in this area (particularly that which explores within species variation) is seriously lacking. Developing a better understanding of the nature of these associations will allow for a broader understanding of trade-offs between certain individual, or species-specific characteristics, and problem-solving capacities.

CHAPTER 8: DISCUSSION

The original studies I presented in this thesis were motivated by the potential psittacine research has to add clarity to debates concerning cognitive convergence and the factors that explain its occurrence. Specifically, the major research objectives I set forth to accomplish included: (1) to contribute to our understanding of parrot social behaviour and cognition by conducting research on two species of which little is known, OWAs and BGMs, and (2) to investigate whether individual variation in cognitive performance may be explained (at least in part) by individual variation in affiliative investment in partnerships. Research objectives were accomplished through an observational investigation of relationship quality, and by conducting experimental studies that investigated inhibitory control, causal understanding, social learning, and cooperative problem solving. Correlational analyses were then conducted in order to determine whether subject affiliative investment and performance on cognitive tasks were related. Boldness as a potential covariate of cognitive task performance was also investigated in BGMs.

In this final thesis chapter, I provide a brief summary of my research findings, followed by a discussion of the implications of my findings. I additionally address limitations that may have influenced results, and provide suggestions for future research and concluding remarks.

Summary of findings

Relationship quality. Findings from the OWA and BGM relationship quality study were consistent with descriptions of Amazons and macaws as possessing social characteristics that are complex and typical of psittacines (Hoppe, 1992; Forshaw,

2006; Renton, 2004). As expected, evidence of pair bonding was found; focal birds in both groups showed selective affiliative investment, engaging in affiliative interactions with specific individuals (preferred partners) more so than other group members (as indicated by composite preferred partner affiliation scores). In the majority of cases, relationships were reciprocal; focal birds and their partners maintained close physical proximity (often in contact), and (for the most part) frequently engaged in allopreening and behavioural coordination and/or synchrony. Some evidence of agonistic support was also found in both species. Overall, OWAs and BGMs showed similar levels of affiliative investment in their relationships, as indicated by the results of between species analyses of composite scores (based on close proximity, allopreening, coordination/synchrony, and courtship feeding). There was a great deal of individual variation in composite scores in both groups. As study groups consisted of group-housed, non-breeding individuals, these findings are consistent with the assertion that psittacines selectively form bonds with conspecifics that are actively maintained all year round (Forshaw, 2006; Hoppe, 1992; Seibert, 2006; Spoon, 2006).

Although OWAs and BGMs were found to be similar in overall affiliative investment and dyad composition (female-male and male-male pair bonds were found in both species), some intriguing differences emerged when individual behaviours were analyzed. While courtship feeding and vent allopreening were observed in approximately half of BGM focals, these behaviours were not observed at all in OWAs. These findings are interesting as courtship feeding and vent allopreening these behaviours are commonly associated with mating and breeding in avian research (Butler, Hazelhurst, & Butler, 2002; Schneider, Serbena, & Guedes, 2006).

Between and within species analyses of focal and preferred partner interactions also revealed that BGMs invested more energy into body allopreening than OWAs,

with OWAs engaging more in head allopreening than body allopreening. BGMs were also found to engage in more mutual allopreening than OWAs. Interestingly though, mutual allopreening was significantly positively correlated to composite affiliative scores in OWAs, but not BGMs. These findings illustrate that allopreening interactions are complex in psittacines, and likely serve various social functions, in addition to hygienic functions.

Performance on cognitive tests. Based on the evidence of high-quality partnerships that was found in OWAs and BGMs, as well as findings from previous investigations of psittacine cognition, one would be justified to expect that competent performance would be seen in both species in most, or all, of the cognitive tests they were given. However, overall, OWAs and BGMs showed limited competency on two of the three physical cognition tasks, and one of the two social cognition tasks.

Inhibitory control. Inhibitory control was tested in OWAs and BGMs using a cylinder task and an A not B task (Chapter 5, Study 1, Experiments 1 and 2). The former tested whether subjects would be able to inhibit the impulse of reaching straight ahead to obtain food from a transparent cylinder (in accordance with the visual feedback of the food's position); correct responses consisted of taking a detour to the side opening of the cylinder. The A not B task tested whether subjects would be able to inhibit behaviour that had been repeatedly reinforced (locating food hidden in cup A on three consecutive trials), and locate food in an alternate location (cup B), after observing its displacement.

In both species, evidence of inhibitory control was found in the cylinder task, but not the A not B task. While some subjects in both groups scored relatively highly in cylinder test trials, OWAs and BGMs did not select the correct cup during A not B test trials at levels greater than expected by chance. It should be noted though, that the

significance of poor performance on A not B tests have been highly debated (Hoffmann et al., 2011), and the findings that were obtained from the cylinder task are more consistent with previous parrot research (Auersperg et al., 2013; Gossette et al., 1966).

OWAs performed significantly better on cylinder test trials than BGMs, and less variance was seen in their performance (OWAs, 4 – 7 correct out of 10 trials; BGMs, 0 – 9). This difference, which was substantial ($r = -.41$), is contrary to what would be predicted by MacLean et al.'s (2014) findings. Comparisons across 36 avian and mammalian species found that absolute brain size accounted for the greatest amount of variance in performance on the cylinder task, and yet OWAs have smaller brains than BGMs (Iwaniuk et al., 2005).

Causal understanding. The causal principle of connectedness was investigated in OWAs and BGMs using two-option means-end tasks (Chapter 5, Study 1, Experiment 3). In the discrimination training phase of the experiment, subjects were presented with strings attached to baited dishes, one string was continuous and the other was not. Birds that met criterion were given transfer tests using different materials and configurations to see if they showed evidence of having acquired the concept of connectedness.

Only two of 12 OWAs, and none of the BGMs ($N = 9$), passed the discrimination phase (birds were given up to 150 trials to meet criterion). Of the birds that failed to meet criterion, one OWA showed evidence of improvement across sessions. No evidence of improvement was found among BGMs, and one BGM's performance was found to decrease across trials. Results from between species analyses showed that OWAs and BGMs performed similarly in string-pulling training trials; no significant differences were found in the proportions of OWAs and BGMs

that met criterion, the percentage of correct responses birds made across trials, or in the maximum number of correct responses subjects made in a session. The two OWAs that passed the discrimination training phase showed no evidence of concept transfer, failing to perform significantly above chance on their 10 transfer test trials.

Due to the extensive number of studies that have demonstrated discrimination learning capacities in avian species, these findings were highly surprising and raise the strong possibility that one or more aspects the method used (e.g., stimuli features and/or set up) may not have been adequate for testing discrimination learning and causal understanding in OWAs and BGMs (or potentially other psittacine species). This finding therefore highlights the importance of giving careful consideration to species specific characteristics (e.g., perceptual capacities) when designing comparative research.

Between species analysis of composite cognitive performance scores. Results from the between species analysis of cognitive performance composite scores (derived from cylinder test trials and means-end discrimination training trials) indicate that there was a trend for OWAs to perform better than BGMs. The medium to large effect size indicates that with a larger sample size this result would probably become significant.

Social learning.

Comparisons of Amazon experimental and control groups. Evidence of social learning was found in OWAs using an open diffusion experiment that tested the spread of a novel foraging technique (see Chapter 6 for details). Three groups (2 OWA, 1 BFA) were tested using a two-action foraging box, including experimental groups exposed to demonstrators using different techniques (slide or pull) and control birds. Although previous studies have demonstrated that psittacines are capable of imitation, in this naturalistic set-up no evidence was found that parrots copied the demonstrated

opening technique; while more experimental birds than control birds interacted with the box and opened it, they were no more likely to use the demonstrated technique than the non-demonstrated one. Locale/stimulus enhancement was therefore the likely mechanism involved in experimental bird performance (and not imitation). Results also indicated that willingness to defend access to the box was important in task acquisition (exhibiting aggression and opening the box were positively correlated). Pilfering food and success in opening the box were also found to be positively correlated; thus, in a group context, pilfering may promote learning of new foraging opportunities.

Comparison of OWA and BGM experimental groups. BGMs were also tested on the two-action task using an open diffusion design (Chapter 7, Study 2). They experienced the same testing procedures as did OWA experimental groups in the study summarized above (Chapter 6); however, only one BGM group was available for study. As BGM performance could not be compared to other BGM groups (experimental and control), conclusions could not be drawn concerning the forms of social learning that may have been involved in their task acquisition. Analyses instead focused on comparing BGM task acquisition to that of the OWA slide experimental group (BGM demonstrators also performed the slide method). BGMs were found to have performed similarly to OWAs; no significant between species differences were found in the proportions of birds that entered the TZ, the proportions of birds that opened the box, or the level of aggression birds exhibited.

Cooperative problem solving. As was the case with the means end task, OWA and BGM performance on the loose string task was surprisingly poor, but this was likely influenced by factors unrelated to cognitive capacity. Of 12 OWAs that began the loose string task, four stopped coming into the testing compartment, and the rest

failed to meet criterion in familiarization trials (phase consisted of three conditions that were progressively more difficult, following Seed et al.'s (2008) procedure). This was unexpected, as all of the rooks that were tested by Seed et al. (2008) were able to meet criterion. However, differences in beak and foot morphology between rooks and parrots may explain why rooks showed less difficulty than OWAs and BGMs in passing the last condition, which required the greatest motor coordination.

Three OWAs and three BGMs ($N = 6$) met criterion and moved onto the testing phase, along with one OWA and one BGM that had failed to meet criterion, but had come close to it. Unfortunately, only one OWA dyad completed testing; BGM testing had to be terminated due to the lack of social tolerance individuals showed towards each other in the testing compartment, and one OWA dyad stopped coming into the testing compartment before completing the simple cooperation test (they did not complete any delayed partner arrival test trials). Thus, in addition to the challenging nature of task requirements during the familiarization phase (in terms of motor skill required), lack of motivation to engage in test trials presented a major challenge in the OWA investigation, and aggression was problematic in the BGM study.

The OWA dyad that completed testing met criterion in the simple cooperative test in 51 trials. These birds therefore showed some capacity to synchronize their behaviour in order to successfully complete a problem that requires coordination. However, the dyad failed all delayed partner arrival trials, indicating that they did not understand the need and role of their partner in successfully completing the task.

Affiliative investment as a potential covariate of cognitive performance.

Although Emery et al. (2007) proposed the relationship intelligence hypothesis to address differences in avian cognition at the species level, it is possible that associations between relationship quality and problem-solving capacities may also exist

at the individual level. Correlational analyses were conducted in order to explore whether individual variation in performance on cognitive tasks may be explained (at least in part) by individual variation in the degree of affiliative investment experimental birds demonstrated in their relationships.

Composite scores that measured focal birds' affiliative investment in their relationships with preferred partners were not found to be significantly related to performance on physical cognition tests, including cylinder test trials, string-pulling discrimination training trials, or cognitive performance composite scores (Study 2, Chapter 5). This was the case when species were assessed separately, as well when OWA and BGM scores were combined. When performance on the social learning task was compared to affiliative scores, a significant relationship was found in BGMs, but not OWAs (reported in Study 3, Chapter 7). In BGMs, frequency of box opens was positively correlated with composite preferred partner affiliation scores.

Boldness as a potential covariate of cognitive performance. An experimental study was conducted that investigated boldness in BGMs through the use of novel object tests (the OWA group was not available for study when this experiment was conducted, thus data collection on OWA boldness was not possible). BGM boldness scores (based on latency to approach measures) were correlated with cognitive test scores in order to examine whether individual variation in this trait may account for variation in performance on cognitive tests (Study 2, Chapter 5).

BGMs showed a great deal of variation in the numbers of subjects that passed each of the five tests and the scores subjects got on each test (see Table 5.8 and Figure 5.5, Study 2, Chapter 5). Overall boldness scores were not found to be significantly related to performance on cylinder test trials, string-pulling discrimination training trials, or cognitive performance composite scores. This was also the case when scores

on each boldness test were individually correlated with cognitive performance; however, analysis results comparing composite cognitive scores to scores BGMs obtained on the lizard test were approaching significance ($p = .068$), indicating that a relationship could potentially exist between boldness and cognitive task performance in BGMs. Further support for this was found when performance on the social learning task was compared to boldness scores. A significant negative relationship was found between overall boldness scores and number of box opens; thus, birds that showed relatively low latencies to obtain rewards during test trials, opened the box more frequently. BGMs that had relatively low overall boldness scores (thus showing low latencies to obtain rewards during test trials) showed greater frequencies of box opens; this relationship was significant.

Bringing it all together – implications of findings, suggestions for future research, and concluding remarks

In recent decades, the scientific community's views on avian cognition have been undeniably transformed by studies of large-brained birds. Corvid and psittacine research not only called into question long held beliefs about the basic nature of avian cognition, but perhaps more significantly, it has impacted our understanding of the evolution of intelligence. Evidence of complex cognition in corvids and psittacines has led to the recognition that mammalian and avian species likely evolved comparable high-level cognitive capacities independently, indicating the occurrence of convergence. Traditional notions of social complexity and its evolutionary relationship to intelligence have also been challenged by avian researchers.

In their proposal of the Relationship Intelligence Hypothesis (RIH), Emery et al. (2007) argue that what has been most influential in the emergence of flexible cognition

(in terms of social complexity) is the nature of the social relationships that animals form. They therefore make the case that quality is more important than quantity in understanding how species' social patterns relate to their cognitive adaptations; the authors note a key similarity that is found in the typical social interactions of large-brained, cognitively complex animals (including corvids, apes, and dolphins) - the presence of bonding and long-term partnerships. In support of their argument, Emery et al. reference research indicating that psittacines, like corvids, form high-quality long-term partnerships, while also showing evidence of cognitive complexity. However, as relatively few psittacine species have been the subject of thorough investigation, particularly in cognitive research, it is unclear how representative these findings are of the Psittaciformes order. The OWA and BGM original research I presented in this thesis was motivated by a desire to expand on our understanding of psittacine social complexity and cognitive capacity, and the potential association that may exist between these two factors.

Significance of findings. The observational study I conducted provides further support for the notion that psittacines develop and maintain partnerships comparable to those found in other animals that have been identified as cognitively complex. Like corvids, primates, and dolphins, OWAs and BGMs showed selective and active affiliative investment in social relationships. Emery et al. (2007) argue that a defining feature of corvid and psittacine social complexity, which distinguishes them from small brained species (e.g., geese and albatrosses), is the high level of energy individuals typically invest in maintaining and strengthening bonds outside the breeding context. Findings from my observational study provide support for this; evidence of pair bonding was found outside the breeding season. Many of the kinds of affiliative behaviours that have been observed in corvid, primate, and dolphin partnerships were

observed in OWAs and BGMs (e.g., maintaining close physical proximity, social grooming, synchrony/coordination, agonistic support). Importantly, these behaviours, which are believed to provide mechanisms through which bonds are formed and strengthened, were observed in non-breeding birds, including same-sex pair bonds. These findings are therefore consistent with the idea that psittacines form alliances that serve important social functions, likely providing benefits that extend beyond breeding success.

As various researchers have argued, identifying and operationally defining behavioural dimensions of animals' social relationships is essential to developing a comprehensive understanding of the fitness implications of relationship quality, including its association to cognitive adaptations (Dunbar & Shultz, 2010; Fraser & Bugnyar, 2010; Spoon et al., 2007). By assessing OWAs and BGMs on a variety of measures (including proximity, affiliative behaviour, and social tolerance), I was able to quantify relationship quality in these two species. The use of individual behaviour and composite indices allowed for the identification of similarities and variation at the species and individual levels. Both species, for instance, showed comparable levels of overall affiliative investment (as measured by composite affiliative investment scores), with both species showing a high degree of individual variation in this measure. As compared to OWAs, BGMs demonstrated additional affiliative behaviours (courtship feeding and vent allopreening). These findings, I believe, may be explained by the relatively low levels of social tolerance that were observed in BGMs. Lower levels of social tolerance, coupled with the potentially lethal beaks macaws have, indicates that mechanisms that allow for the de-escalation of agonistic encounters, or for trust to be built, may be of particular importance to macaws as compared to other psittacines that differ in these traits (like OWAs). Evidence of the use of social grooming as a means

of de-escalating aggression has been found in other avian species (e.g., common guillemot, Lewis et al., 1997), as well as in primates (e.g., Java monkeys, Schino et al., 1988). Vent allopreening may be particularly effective in reinforcing the pair bond, as this highly sensitive area is known to be the target of aggressive behaviours in some avian species (Hughes & Duncan, 1972). In OWAs, mutual allopreening (when partners simultaneously preen each other) was found to be significantly positively correlated with affiliative investment. To my knowledge, this the first piece of evidence that mutual allopreening measures may serve as good indicators of bond strength in OWAs, as appears to be the case in chimpanzees (Fedurek & Dunbar, 2009).

Empirical comparative investigations, such as the OWA and BGM observational study I conducted, make it possible for a range of hypotheses to be tested concerning sociality and its functions. It has been suggested (and some evidence has been found), for instance, that relationship quality variables may be predictive of offspring survival rates, predatory defence success, or the ability to acquire and protect resources (Möller et al., 2001; Spoon, et al., 2006; Silk, et al., 2003; Treves & Chapman, 1996). In order to develop a comprehensive understanding of the implications of relationship quality for individual and group fitness, a comparative framework is needed that identifies and defines behavioural expressions of affiliative relationships in a variety of species (Dunbar & Shultz, 2007, 2010; Emery, Clayton, & Frith, 2007; van Horik et al., 2012). As I demonstrated in the correlational analyses I presented in Chapters 5 and 7, relationship quality measures can also be used to test social intelligence hypotheses.

Through physical and social cognitive tasks, I explored capacities in OWAs and BGMs that have been associated with flexible problem solving (which is considered a

hallmark of intelligence, Emery & Clayton 2004; Humphrey, 1976; Roth & Dicke, 2005; van Horik et al., 2012). The cylinder task experiment I conducted provides initial evidence of inhibitory control capacities in OWAs and BGMs, with OWAs significantly outperforming BGMs. Additionally, evidence of social learning was found in OWAs (conclusions could not be drawn regarding the social learning processes that may have been involved in BGM social learning task acquisition). Contrary to what was expected, performance on the other two physical cognitive tasks (A not B and means-end string pulling), and the cooperative problem solving task, was poor in both species. As psittacines are widely recognized as birds that show evidence of cognitive complexity, and share many of the traits that are found in other intelligence animals (e.g., social complexity, large brains, long developmental periods, long life histories), the difficulty they showed with these tasks was surprising.

This apparent inconsistency, between descriptions of psittacines as cognitively complex and OWA and BGM cognitive task performance, raises important theoretical and methodological issues relevant to the investigation of cognitive capacities in non-human species. As MacLean and colleagues (2012, 2014) note, understanding the evolution of intelligence is not only one of the primary objectives of comparative psychologists, but also one of the most challenging research objectives scientists have undertaken. They argue that in order to make meaningful progress towards attaining this goal, a wide range of species need to be tested on the same problem solving tasks, using similar procedures. MacLean et al. (2014) demonstrated the value of this approach; in a comparative investigation that included assessing 36 species' performance on cylinder and A not B tasks, they found evidence that brain expansion was key to the evolution of inhibitory control (OWA data I collected and reported in Chapter 5 contributed to MacLean et al.'s findings). Although this approach (testing

different species using the same experimental paradigms) is highly valuable because it allows for the testing of broad hypotheses about the evolutionary origins of mental processes, it has limitations.

One of the criticisms that has been levied against the practice of using similar experimental paradigms to test different species' cognitive capacities, is that this approach often fails to consider important factors, such as how ecologically relevant the task is to the species being tested, or how species-specific non-cognitive adaptations (e.g., perceptual skills) may influence task performance (Emery, 2006; Shettleworth, 1998). While the tasks that I tested OWAs and BGMs on are valuable in that they can be (and have been) used to test a range of species, they are limited in these two important ways. It is possible that the poor performance observed in OWAs and BGMs in the A not B, string pulling, or cooperative tasks could be explained (at least in part) by the fact that these tasks are not particularly relevant (ecologically or socially) to these birds. Furthermore, as previously indicated, it is possible that visual perception or morphological features typical of parrots may have negatively impacted performance on cognitive tasks (e.g., spatial resolution abilities may have interfered with discrimination learning; bill shape and toe composition may have interfered with birds' ability to meet criterion in cooperative task familiarization trials).

The research limitations identified above are relevant to theoretical debates reviewed in Chapter 1, concerning anthropocentric versus ecological approaches to animal cognition and whether animal cognition is best understood through general processes models or modular models of cognition. Highly controlled, lab-based experimental investigations that aim to measure general processes (e.g., discrimination learning) have been criticized as anthropocentric (Emery, 2006). The notion that cognition in non-human species is composed of various highly specialized domain-

specific mechanisms has gained popularity in recent years (Shettleworth, 2012). This perspective considers species' unique evolutionary histories and encourages researchers to take an ecological approach to comparative research; it can be argued that considering the specific types of problems animals are likely to encounter within their natural environment provides the best opportunity to devise research paradigms that tap into domain-specific cognitive adaptations that may be complex. As comparative researchers interested in understanding the nature and origins of intelligence, we are faced with the challenge of having to balance the need to create paradigms that can be used to test a range of species (with little modification so that results are comparable across species), with the need to devise tasks that are ecologically relevant to the species being tested and also take into account species specific adaptations (non-cognitive) that may influence results.

Although not free from limitations, I believe that the open diffusion social learning study I ran (reported in Chapters 6 and 7) serves as a good example of an experimental design that can be used to test various social species in a controlled and ecologically relevant manner. As discussed in Chapter 6, much of the evidence of social learning in wild animals that has been reported focuses on the occurrence of within species group-specific variations of behavioural patterns, often in the area of foraging. For species that are social foragers (like OWAs and BGMs), dyadic testing in highly controlled environments is not ecologically relevant (particularly when a demonstrator and an observer are physically separated). While the open diffusion design is relatively unconstrained, it much more closely resembles circumstances that social foragers are likely to encounter in a natural context; and while it poses challenges to interpreting findings (e.g., identifying who learns from whom, or determining whether failure to find evidence of imitation is best explained by cognitive

limitations or social distractions present in the open diffusion set up), it also allows us to identify non-cognitive factors that are likely present in the natural environment and may influence the acquisition of a novel foraging technique; in OWAs, for instance, evidence was found that aggression and pilfering were positively correlated with task acquisition.

It has been widely argued that gaining a true understanding of the factors or conditions that promote complex cognition requires correlational research that not only compares cognitive task performance to species specific characteristics, but also assesses potential associations between task performance and individual traits (Bond et al., 2007; Carere & Locurto, 2011; Cussen & Mench, 2014; MacLean et al., 2012). As previously discussed, the Relationship Intelligence Hypothesis proposes that active investment in the maintenance of stable, cooperative partnerships may be associated with flexible, high-level cognitive capacities (Emery et al., 2007). While there is compelling evidence that differences in cognitive capacities between avian species may be explained (or influenced) by relationship quality variables (Emery, 2006; Emery et al., 2007; Dunbar & Shultz, 2010; Zorina & Obozova, 2012), it is unclear whether this may also be the case at the individual (within species) level. In order to address this, I investigated whether effort invested in relationship maintenance (based on data collected in the observational study reported in Chapter 4) was correlated with cognitive task performance (cylinder test trials, string-pulling discrimination training trials, composite cognitive scores, and two-action box task). These analyses were undertaken because I believe that the capacities the tasks were aimed at measuring (inhibitory control, discrimination learning, and social learning) are relevant to relationship maintenance (e.g., inhibitory control might allow individuals to be more flexible in their interactions with their partners; discrimination learning allows

individuals to distinguish between partner and non-partner contact calls; social learning allows individuals to acquire information from partners' behaviour).

To my knowledge, my investigation has yielded the first piece of evidence that in some psittacines, affiliative tendencies may influence or covary with performance on cognitive tasks at the within species level; BGMs that had higher composite preferred partner affiliation scores were significantly more likely to open the two-action box in the social learning task. This finding is consistent with the idea that factors such as the capacity to attend to social cues or motivation likely play roles in both the capacity to acquire information from others, and the ability to maintain affiliative relationships. However, no evidence of this association was found in OWAs; results indicated an extremely weak relationship between these factors, suggesting that a small sample size is not likely a plausible explanation for failure to find a significant correlation. Further research is needed to determine whether these findings are representative of species differences. No evidence was found that composite affiliative scores were correlated with performance on the cylinder task, string-pulling discrimination training trials, or composite cognitive scores in either species. As I believe my investigation had limitations that may have impacted performance on these tasks (limitations are discussed in more detail in Chapter 5's general discussion and addressed further later on in this chapter), one should not conclude that affiliative variables are not associated with physical cognition in these species; this too will need further investigation.

In BGMs, evidence was also found that social learning task acquisition was also correlated with individual variation in boldness; individuals that showed greater levels of boldness (as indicated by lower latencies to obtain rewards) were found to open the box more frequently. This finding is consistent with descriptions of bold individuals as showing relatively high levels of object exploration (Fox & Millam, 2006; Frost et al.,

2007), and indicates that in foraging context, boldness is highly adaptive; this trait likely increases an individual's chances of learning how to exploit novel food sources. However, it should be noted that although overall boldness scores (based on latencies to approach for 5 test objects) were found to be significantly correlated to box opens, highest latency test object scores were not. This is interesting as this was the only boldness measure that was found to show a correlational trend with performance on physical cognitive tasks (as measured by composite cognitive scores). This relationship was not significant, but the sample size was small ($N = 7$); it is therefore possible that a significant correlation may have been found with a larger sample size. It is unclear why overall boldness scores were found to be correlated with box opens, while highest latency test object scores were not. These findings, however, indicate that this 'personality' trait may be an important characteristic to consider when drawing conclusions about the problem solving capacities of BGMs (and potentially other psittacine species).

General research strengths and limitations. I believe that one of the strongest aspects (in terms of scientific validity) of the original research that I presented in this thesis is the fact that the subjects I collected data on lived in semi-natural conditions. This allowed OWAs and BGMs to self-select partners and engage in a range of social interactions. Observing psittacine social behaviour in these captive conditions, it has been argued, provides the best opportunity to obtain findings that are representative of what would likely be observed in wild populations (Spoon et al., 2006). The individual variation that was observed in OWA and BGM focal birds' affiliative investment, indicating variations in pair bond strength, support this assertion. As previously stated, the range of relationship quality measures that I used also made it possible to identify variation between OWAs and BGMs that may be representative of

between species differences in behaviours that could be critical to relationship maintenance or stability (e.g., allopreening or social tolerance).

Unfortunately, the fact that my research subjects largely consisted of pair bonds that showed strong affiliative relationships may have meant that the propensity for distraction during testing was relatively high, impacting cognitive test performance. In order to be tested, birds had to physically separate from their partners. Although they showed willingness to complete test trials, they may have been motivated to complete test trials rapidly to re-join their partners; additionally, vocalizations from their partners (or other birds) may have distracted them during testing (anecdotal, birds often looked up and adopted postures that indicated alertness when loud vocalizations were emitted by group members).

As discussed in Chapter 5, there are additional limitations associated with subjects' living conditions that may have influence performance on cognitive tasks, and should be acknowledged. For instance, OWAs and BGMs lived in relatively stimulating and enriching environments (socially and physically), and engaging in the physical tasks they were presented with may not have been particularly rewarding for them. The fact that birds had access to a varied, high quality diet may have also influenced their food motivation during testing. It is also important to consider the potential impact that subjects' individual histories may have had on their performance. As these birds were former pets, it is likely that many (or most) of them had experienced impoverished environments at some point in their histories; experiencing a lack of social or physical stimulation is widely known to have significant negative consequences for cognitive development (Davenport et al., 1973; Fox & Millam, 2004; Lapiz et al., 2003; Novak & Sackett, 2006). Additional factors I discussed in Chapter 5 that may explain (to some degree) poor performance are visual perception issues (e.g.,

the use of artificial light that may produce a stroboscopic effect, stimuli that did not have strong visual contrast) and the fact that observation periods were not part of testing procedures, which would have provided subjects with more opportunity to study stimuli set up before responding.

Directions for future research. Due to the limitations identified above, OWAs and BGMs will have to undergo additional testing in order to determine the extent to which they possess inhibitory control, means-end, social learning, and cooperative problem solving capacities. Additional cognitive testing will also allow for further investigation of the potential associations that may exist between cognitive complexity and social complexity (or personality traits) in psittacines. I believe there is value in this research as it allows for a broader understanding of trade-offs that may exist between certain individual, or species-specific characteristics, and problem-solving capacities. Based on the challenges that OWAs and BGMs experienced in some tasks, future parrot researchers should carefully consider species-specific traits (e.g., morphology, perceptual abilities, temperament) when designing or adapting research paradigms. This is one of the challenges of investigating species of which little are known, but is vital for the accurate collection of data.

As such few avian species have undergone thorough investigation, avian research must continue to be expanded. Social intelligence hypotheses, for example, can also be tested by investigating species of raptor. There are over 300 raptor species (Burton, 1989), and as is the case with parrots, very little is known about most of them when it comes social behaviour and cognition. Although research on these birds is limited, there is evidence of social complexity in some species. Harris hawks, for instance, are known to live in stable social groups primarily composed of related individuals (Ellis, Bednarz, Smith, & Flemming, 1993; Snyder & Snyder, 1991). It has

been noted that while these birds show a high degree of aggression towards non-group members, they show high levels of social tolerance towards group members. Group members also engage in cooperative hunting (Ellis et al., 1993). Cooperative hunting has also been documented in eagles and osprey (Ellis et al., 1993; Flemming, Smith, Seymour, & Bancroft, 1992; Folk, 1992). Furthermore, evidence of social learning in the acquisition of hunting skills has been found in field studies of juvenile Marsh harriers (Kitowski, 2009). In terms of brain size, owls have been found to possess among the largest and most complex brains among avian species (Zorina & Obozova, 2012). These findings suggest that raptors, like parrots and corvids, may serve as valuable subjects in studies that aim to investigate potential evolutionary associations between social factors and cognitive capacities.

Concluding remarks. Although I believe that much of the poor performance OWAs and BGMs demonstrated was primarily caused by non-cognitive factors, it is a reminder that although evidence of complex cognition has been found in some parrots, there is a great deal we still do not know about parrot cognition. As there are more than 200 psittacine species, and only a small number of individuals from a handful of species have been empirically studied, it is prudent to be conservative when making generalizations about how pervasive complex cognition is throughout the order. It is possible, for example, that significant differences may exist in species that evolved in different regions of the world (e.g., Australian species like cockatoos, versus neotropical species like Amazons and macaws).

While there is still much that needs to be learned about psittacines, what we do know about these birds gives us reason to believe that psittacine research has the potential to make significant contributions to our understanding of evolutionary relationships between social factors and cognitive adaptations. Based on research

findings (including the observational findings I presented in this thesis), one can conclude that psittacines serve as strong examples of non-human species that demonstrate a high degree of social complexity. Research findings also suggest that they serve as examples of the occurrence of convergence in the cognitive domain. It is therefore essential that psittacine research continues to be undertaken and expanded. The original research I presented in this thesis, which I believe is the first comparative study of relationship quality and cognition in macaws and Amazons, contributes to this effort. My findings provide evidence of high-quality relationships in these species, as well as inhibitory control and social learning capacities; furthermore, it has yielded evidence of potentially meaningful between species differences in social behaviour and cognitive capacity.

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