Comparative Avian Cognition: Physical and Social Problem Solving in Corvids and Parrots

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Abstract

Within the last few decades, investigations of problem solving in avian species such as corvids have challenged the few that complex cognitive abilities are unique to the primate lineage, and provide a compelling case for the convergent evolution of cognition in a range of large-brained, socially complex species. Despite these advances, there is still much that is unknown about how corvids acquire and use information to solve problems in both their social and physical environments, and comparably little research has focused on other large-brained avian taxa such as parrots. The research presented in this thesis investigates both physical and social cognition in two parrot and two corvid species by examining how individuals interact with and acquire information about their physical world, and whether birds will use physical information to benefit conspecifics. Observational data provide new evidence for a novel form of tool use among a highly explorative species, the greater vasa parrot (*Coracopsis vasa*), and empirical data show that exploration may provide these birds with information about how novel objects (including potential tools) behave. An additional experiment with kea (*Nestor notabilis*) and New Caledonian crows (*Corvus moneduloides*) suggests that information acquired during exploration may aid in problem solving, although individuals do not change their exploratory behaviour in order to acquire functional information about objects that is relevant to a specific task. An investigation of social cognition in ravens (*Corvus corax*) shows that subjects can attend to multiple dynamic stimuli in order to obtain a food reward, but do not use this ability to provide food to an affiliate or non-affiliate partner. Taken together, the results of these studies suggest that both parrots and corvids are adept at attending to and learning about different types of physical information which can aid problem solving, but do not intentionally seek this information or use it to benefit others.

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Author's Declaration

This thesis contains original work that was carried out by the author, Megan Lambert, under the supervision of Dr Katie Slocombe. The work in this thesis has not been submitted for examination at this or any other institution for another award.

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Chapter 1. General Introduction

The evolutionary origins of complex cognition have been a topic of fascination since the time of Darwin (Darwin 1859, 1871). All animals, including humans, are constantly faced with a vast array of sensory information, which they must selectively attend to and learn from in order to survive and reproduce, but how animals store and process this information varies widely across species (Shettleworth 1998). Associative learning is one universal process by which individuals form associations between stimuli, or between a stimulus and their own behaviour (e.g., dropping a nut on stone results in a food reward; Heyes 2012). In more variable environments where these stimuli are often changing, individuals may benefit from the ability to abstract general rules from these associations and flexibly apply them to novel contexts (e.g., dropping a nut on any hard surface will break it open, or any hard object such as a stone can be used as a tool to break open the nut; Shettleworth 1998; Premack 2007). This cognitive complexity, which is generally defined as the ability to use information flexibly in order to solve a range of novel problems (in contrast to relatively inflexible cognitive adaptations restricted to a single goal; Shettleworth 1998; Premack 2007) seems to reach exceptional levels in humans, and has allowed us to dominate nearly every corner of the globe. Since Darwin's time, a central focus of research has been to understand how the extraordinary cognitive abilities of our own species, *Homo sapiens*, evolved. These efforts have typically focused on nonhuman primates due to their close phylogenetic relationship with humans. Within the last several decades, however, research on species outside of the primate order has challenged the traditionally held notion that complex cognitive abilities are unique to primates, and consequently presented a case for the convergent evolution of cognition in distantly related species that face similar social and ecological pressures.

By examining parallels in the social and physical challenges faced by different species and how these correspond with cognitive performance, it is possible to pinpoint the selective pressures that drive the evolution of cognitive complexity (Shettleworth 1998; Emery & Clayton 2004; Van Horik *et al.* 2012). Research with several avian taxa, including corvids and parrots, has presented a particularly striking case for the convergent evolution of cognition in large-brained and socially complex species. The original work presented in this thesis investigates how both corvids and parrots respond to challenges in their physical and social environments in order to generate insight into the evolutionary origins of cognitive complexity. The current chapter serves to provide a historical and theoretical framework for the empirical research presented in this thesis, and continues into Chapters 2 and 3 with a more focused review of the specific behaviours and cognitive processes that will be examined.

A brief history of comparative cognition

In his book the *Descent of Man*, Darwin was one of the first to explicitly address the evolution of the animal mind by spending a significant portion of his book comparing the mental abilities of humans and other animals. In his discussion, Darwin provided primarily anecdotal evidence that nonhuman species seem to exhibit many of the characteristics which are believed to define humans including tool use, curiosity, imagination and imitation, all of which have since become vast fields of research within the broader field of comparative cognition (Darwin 1871).

Several years after this Lloyd Morgan published his seminal text, *An Introduction to Comparative Psychology* (Morgan 1903), in which he used a markedly different approach for describing behaviour which specifically rejected the anthropomorphic tones used by others such as Darwin (e.g., when describing maternal instinct: “one female baboon had so capacious a heart that she adopted young monkeys of other species”; Darwin 1871, p41). In what is now famously referred to as Lloyd Morgan’s Canon (Shettleworth 2010), Morgan stated that “in no case is an animal activity to be interpreted in terms of higher psychological processes if it can be fairly interpreted in terms of processes which stand lower in the scale of psychological development” (Morgan 1903, p59).

This set the tone for the next few decades of research, with behaviourists such as Watson (1930) and Skinner (1965) explaining animal learning primarily in terms of stimulus-response associations, or associative learning (Hulse 2012). It wasn’t until the 1970s that researchers began to question whether nonhuman animals, namely primates, also possessed ‘higher-order’ mental faculties such as a Theory of Mind (Premack & Woodruff 1978) or linguistic capability (Premack 1971). Since this time the field of comparative cognition has grown exponentially, and is constantly incorporating new species into its comparative framework which were virtually absent from cognitive research until only decades ago (e.g., carnivores: Vonk & Johnson-Ulrich 2014; Holekamp *et al.* 2007; cetaceans: Guentuerkuen 2014; invertebrates: Roth 2013).

Generally speaking, studies of animal cognition are aimed at uncovering how animals gather, process and respond to information in their environment (Shettleworth 1998, p4). These abilities are generally related to an individual's social or physical environment (see Table **1** for a summary of the key challenges in these domains and how animals respond to these challenges in the wild). Within the social environment, animals must compete with conspecifics in order to gain access to resources or mating opportunities, and thus how animals attend to and use social information to interact with other members of their species has significant fitness consequences (Byrne & Whiten 1989). Within the physical environment, animals must learn to efficiently navigate their environments, remember the location of different food sources and find ways of obtaining food that may be otherwise inaccessible (Shettleworth 1998). Animals may solve problems in both of these domains by learning specific associations or behaviour patterns (e.g. smashing a mollusc on a rock provides food). Species that are able to generate more abstract rules from this information and flexibly apply these rules to solve novel problems are often classified as 'intelligent', however this term has also garnered criticism for its anthropomorphism, as the scale against which all species' cognitive abilities are measured is our own, despite vastly different morphological and ecological adaptations between humans and birds, for example (Menzel 1986; Shettleworth 1998). As Menzel aptly noted in an early review, "trying to arrive at an airtight definition of intelligence is as thankless a job as trying to define 'Life' or 'Man'" (Menzel 1986, p167); thus, in lieu of 'intelligence', the term 'complex cognition' is used throughout this review.

Although the field of comparative cognition encompasses research that focuses on a vast range of cognitive abilities, the results of these studies are often related back to two much broader (and often controversial; Menzel 1986) questions: to what extent are human-like cognitive abilities found in other species, and what does this tell us about the evolutionary origins of (human) intelligence?

General methods for studying animal behaviour and cognition

Unlike other bodily operations (e.g., respiration), cognitive processes cannot be directly observed in terms of physiology. The field of comparative cognition therefore deals explicitly with these unobservables by inferring cognitive processes from an animal's behaviour (Wasserman & Zentall 2009) after ruling out alternative, simpler explanations for that behaviour (Morgan 1903). The study of animal behaviour and cognition addresses these processes using two different, complementary approaches.

The first of these approaches, which was in favour as early as Darwin's time, is an anthropocentric approach focused on understanding the generality of cognition by examining mental continuity in humans and other animals; or in other words, the extent to which other species demonstrate human-like cognitive processes such as memory and theory of mind that underpin human cognition (Darwin 1871; Wasserman & Zentall 2009). This approach is aimed at understanding the evolutionary origins of human cognition, and allows scientists to make inferences about the origins of particular mental processes and when in our evolutionary history they might have evolved. The second approach, which is generally termed the ecological approach, is aimed at understanding the drivers of complex behaviours observed in different organisms in the wild, and therefore considers the question of cognition from a species-specific perspective in order to understand how cognitive processes have been adapted to function within a species' given environment (Shettleworth 1998).

These approaches both rely on both observational and experimental data, usually collected from wild and captive settings, respectively (but see Slocombe & Zuberbühler 2005 and Cheney & Seyfarth 1990 for examples of experiments conducted in the wild). Researchers focusing on animal behaviour in the wild typically collect observational data that may elucidate the function of behaviour in an ecologically valid context, and in particular when other competing forces are at work such as the need to forage and be vigilant against predators (Pritchard *et al.* 2016). One major drawback of studying animal cognition in the wild, however, is that it is often difficult to rule out alternative explanations for behaviours due to the number of uncontrollable factors in nature. For example, many animals gather and store (or cache) food for future consumption, but whether this reflects an innate, species-typical behaviour or more complex cognitive processes such as future planning or episodic memory is difficult to elucidate from observation alone.

Such questions can be addressed through carefully controlled experiments, which if conducted in captivity can be informed by knowledge of the subject's history and previous experiences. These experiments can additionally allow for factors such as hunger level, time of day and proximity of social partners to be controlled and manipulated depending on the needs of the study. For example, in the case of food-caching, laboratory studies have revealed that at least one food-caching species, the western scrub jay, seems to anticipate its future needs when caching, and adjusts its caching strategies depending on the presence of potential thieves (Dally *et al.* 2006; Raby *et al.* 2007; Dally *et al.* 2010; Grodzinski & Clayton 2010). Additionally, captive subjects can be trained on tasks involving the use of manmade objects (e.g., touch screens; O'Hara *et al.* 2015) that would not otherwise be possible in the wild, due in part to practical difficulties of testing individuals in isolation, as well as ethical restrictions associated with provisioning wild animals. Despite their advantages, the novel setups used in captivity, which are always designed from a human perspective, have often been criticized for failing to take into account the morphological or perceptual differences of other species. Additionally, although captive research can demonstrate the cognitive capabilities of a species, it provides little information on how and whether these abilities might function in a natural context (Morand-Ferron *et al.* 2016). Despite these limitations, captive experiments remain a critical means for understanding cognition from either a human-centric or species-centric viewpoint.

Cross species comparisons: analogy versus homology

Regardless of the setting in which it takes place, the ultimate aim of carrying out research with different species across the animal kingdom is to enable the data to be considered from a larger, phylogenetic perspective. By determining whether specific cognitive or behavioural traits exist in closely- or distantly-related taxa it may be possible to trace how ancestral that trait is within a particular clade and the environmental pressures that drove its selection. This homology versus analogy approach has been widely used within the field of biology since the 1900s (although mentioned by Darwin in his first text; Darwin 1859) specifically for investigating the evolution of various morphological traits, but it can be adapted to study of a range of characteristics. The most famous example of this approach is when considering the evolution of forelimbs. The forelimbs of all tetrapods, for instance, are divided into three segments and follow the same developmental pathways (Young & Hallgrimsson 2005). These structures are therefore homologous and were likely present in the last common ancestor of all tetrapods. In contrast, although birds and bats both possess superficially similar wings, these structures are analogous, having convergently evolved in response to similar selection pressures rather than common ancestry. Thus, while homologous traits allow us to answer *when* a particular trait evolved, analogous traits allow us to answer the question of *why*. In terms of cognition, these convergent traits may be particularly informative for understanding the selective pressures that drove the evolution of cognition (MacLean *et al.* 2012).

Prior to the 1990s, studies of animal cognition tended to focus on nonhuman primates due to their phylogenetic proximity to humans. The implicit aim of these studies was to determine the degree of mental continuity (or the homology of different cognitive traits) between humans and apes, which in turn would inform hypotheses about when human-like cognitive abilities evolved (Povinelli & Bering 2002). Questions remaining from this early research, however, included whether such abilities were limited within the primate order, and how such abilities might have been selected for across evolutionary time.

The convergent evolution of cognition

Although avian models had been used in research since the early 1900s, these studies typically focused on associative learning processes rather than asking questions about language or Theory of Mind that were beginning to drive research on primate cognition. Additionally, the model species used were generally birds such as pigeons, quail or chickens. We now know these species are relatively poor candidates for studies of complex cognitive processes due to their small relative brain size and lack of brain structures related to higher-order cognitive processes (Emery & Clayton 2005; Emery 2006). Furthermore, although ornithologists spent extensive time studying a range of species in their natural environments, in a similar way to field primatologists, they tended to focus on behavioural ecology rather than cognitive abilities (Tomasello & Call 1995; Shettleworth 1998; Emery 2006).

Anecdotes of complex behaviour in large-brained birds such as corvids have existed from around the 1800s (Ratcliffe 1997), but it wasn’t until 100 years later in the 1990s that research began to test whether corvids demonstrated complex cognitive abilities such as insight under controlled conditions (Heinrich 1995). Continued research on members of the corvid genus such as ravens, crows and jays began to reveal that these birds show similar performance to primates on tests of cognition including Theory of Mind, future planning and complex physical problem solving (Weir *et al.* 2002; Seed *et al.* 2006; Clayton *et al.* 2007; Raby *et al.* 2007; Bugnyar *et al.* 2016). This research points to a striking case of convergent evolution between two groups with unique evolutionary histories, which last shared a common ancestor roughly 300 million years ago (Emery & Clayton 2004; Emery 2006).

One outstanding and intriguing question is what drove the evolution of these analogous cognitive abilities? Despite their phylogenetic distance, corvids and primates share a number of biological and ecological similarities which have been cited as factors related to cognitive development (Van Horik *et al.* 2012). Most importantly, both corvids and apes are relatively altricial species which show a prolonged period of development, during which they remain dependent on their parents and gain additional opportunities to learn from conspecifics. In terms of ecology, they are both omnivorous, generalist feeders that rely on patchy and ephemeral food sources, and often engage in extractive foraging such as nutcracking or extracting insects from bark. Finally, both corvids and apes operate within dynamic social environments that are characterized by complex relationships between group members (Emery 2006).

More recently, additional research has reported similarly complex physical or social problem solving among other species including cetaceans, elephants and social carnivores such as hyenas (Marino 2002; Holekamp *et al.* 2007b; Holekamp *et al.* 2007a; Marino *et al.* 2007; Byrne *et al.* 2009). Dolphins and elephants, for example, are among the few species (including primates) that are known to pass the standard test of mirror self-recognition (Reiss *et al.* 2001, Plotnik *et al.* 2006; but see Harley 2013). Studies of hyenas have shown that these animals are able to track third-party relationships among other members of their groups (Holekamp *et al.* 2007a). Like corvids and apes, all of these species live in cohesive social groups (that may also be characterized by fission-fusion grouping patterns) that are often hierarchically structured and feature both agonistic and affiliative relationships among individuals (Emery *et al.* 2007b), providing strong evidence for the validity of the Social Intelligence Hypothesis outside of the primate order (but see Holekamp *et al.* 2007 for a critique).

The Social Intelligence Hypothesis, or Machiavellian Intelligence Hypothesis (Jolly 1966; Humphrey 1976; Byrne & Whiten 1989), was originally proposed to the explain variation in cognitive abilities between different species of primate, ultimately concluding that the complex physical and social cognitive abilities observed in particular species of primate evolved in response to the pressures associated with living in a complex social environment. Debates continue as to what characterises a socially complex environment, with both the quantity and quality of relationships with others being highlighted as important in different taxa (Dunbar 1998; Dunbar & Shultz 2007; Emery *et al.* 2007a). However it seems clear that in these dynamic social environments, the ability to acquire, store and flexibly utilize social information to solve problems could confer numerous fitness advantages, in particular by determining access to food and mating opportunities (Byrne & Whiten 1989; Tomasello & Call 1995).

The neuroanatomy of complex cognition

If complex social environments select for more sophisticated cognitive processes, it follows that this would require greater neural processes, which consequently should be manifested in the brain in terms of overall size of the brain and/or areas involved in complex information processing (Dunbar 1998). In terms of relative brain size (compared to body size), for example, primate, human and cetacean brains are larger than those of other mammals (Jerison 1973). This increase in size is due mainly to the large expanse of neocortex, which in humans plays a key role in learning and other executive processes (Dunbar 2003). In primates, hyenas and bats neocortical volume correlates strongly with social variables such as group size (Dunbar & Bever 1998), grooming clique size and the frequency of social play (Lewis 2000).

There are also some notable exceptions to this rule, however. For example, many ungulate and bird species travel and forage in large herds or flocks of over 100 individuals, but group size in these species only inconsistently predicts either brain size or neocortex/forebrain size (Beauchamp & Fernandez-Juricic 2004;

Shultz & Dunbar 2006). Similarly, many of the avian species which show the highest performance on cognitive tasks are those which show low average group sizes (e.g., many corvid and parrot species typically form strong monogamous pair bonds). Rather than overall group size, a key predictor of brain size and cognitive ability may instead be the quality of social relationships formed by individuals within a group, which is typically measured in terms of investment in affiliative behaviours such as food offering, allopreening and aid in agonistic interactions (Emery *et al.* 2007a). The frequency of these behaviours within a dyad can then be used to form a measure of the quality, or 'strength' of the relationship. Variation in relationship quality amongst dyads in a group can be effectively investigated with social network analysis, and sociograms used to illustrate the relative strength of dyadic bonds, with dyads who engage in more affiliative behaviour connected with thicker lines (see Emery *et al.* 2007 for an example). In long term monogamous relationships, individuals may benefit more from the ability to attend to subtle social signals and changes in their partner's behaviour in order to respond appropriately and maintain their partnership. Indeed, among both ungulates and birds, the strongest predictors of brain or neocortex/forebrain size are the complexity, or quality, of social relationships within the group, which is consistent with the Social Intelligence Hypothesis (Shultz & Dunbar 2006; Emery *et al.* 2007a).

The avian brain was historically characterised as a relatively simple structure derived from the basal ganglia and therefore incapable of producing flexible behaviour (Emery & Clayton 2005). Instead, it has since been established that the avian forebrain, or the nidopallium, is derived from the pallium in the same way that the mammalian neocortex is (Güntürkün & Bugnyar 2016). Additionally, despite their small absolute size, the brains of corvids and parrots possess significantly more neurons in the forebrain than most mammals (Olkowicz *et al.* 2016). The ultimate implications of this marked similarity in structure and function between two very divergent brain structures suggest that they were ultimately shaped by similar evolutionary pressures favouring similar cognitive processes.

Future directions for the study of complex cognition

The research presented thus far provides evidence for the convergent evolution of complex cognition in a range of nonhuman species and suggests that these cognitive abilities are associated with several life history traits including a dynamic social environment and a slow developmental period in which juveniles may learn from other group members, as well the relative size of the neocortex in mammals or the nidopallium in birds. The majority of research focusing on animal cognition has historically centred on primates, however studies outside of the primate order, and particularly with corvids, suggest that these large-brained birds are ideal for studies of social and/or technical intelligence.

Despite this shift in focus, we are far from understanding the mental lives of corvids and other birds to the same extent that we understand the primate mind (see Table 1 for an outline of some of these knowledge gaps). Studies of parrots, for example, are only in their infancy but suggest that parrots are a promising avenue for future cognitive studies (see Huber & Gajdon 2006 and Auersperg *et al.* 2013 for examples). Further research on both of these groups is needed in order to fully understand how these species process and use information in their environments, which may ultimately inform our understanding of the selective pressures that drove the evolution of complex cognition in various animals, including humans.

Table 1. Challenges faced by birds in the wild, in either the physical or social domain. The 'current understanding' column details what we currently know about how animals respond to these challenges in nature, and the 'knowledge gaps' column describes aspects of cognition relating to these challenges that are poorly understood.

	Physical Environment	**Social Environment**
Challenges faced in the wild	• Navigating the environment • Obtaining food	• Competition for access to mates and resources
Current understanding	• Repeated interaction with objects in the physical environment affords learning opportunities (Power 2000) • A few birds species use external objects as tools to access otherwise unobtainable food (Shumaker *et al.* 2011) • Many species which use tools are also those that	• Access to these resources can be determined by affiliative relationships, or strong bonds between individuals (Byrne & Whiten 1989) • These bonds are characterized by prosocial behaviours between individuals (e.g., agonistic support or preening; Silk & House 2011)

	frequently explore objects (Power 2000)	
Knowledge gaps	• Do birds learn about objects through exploration? • Do birds explore objects strategically to gain information?	• Do prosocial behaviours reflect a psychological predisposition to benefit the welfare of others? • Are these prosocial behaviours influenced by the identity or behaviour of the recipient?
How this thesis addresses knowledge gaps	• Systematically examines the role of exploration in learning about object affordances	• Examines whether birds show prosocial preferences, and what factors influence these preferences

Thesis outline and aims

As mentioned earlier in this chapter, the cognitive challenges that species encounter on a day-to-day basis typically occur within two separate, but often overlapping arenas: the physical environment, and the social environment. The research presented in this thesis focuses on how different corvid and parrot species respond to and solve these challenges.

Chapter 2. Physical cognition: Tool use, problem solving and object exploration. This review chapter provides a theoretical background for the empirical work on tool use and object exploration presented in Chapters 4 and 5 by reviewing our current understanding of how animals solve problems in their physical environment through the use of tools, including what cognitive abilities underlie tool use and how animals may come to acquire knowledge about potential tools through object exploration.

Chapter 3. Social cognition: Prosocial preferences in nonhuman animals. This review chapter provides a theoretical background for the empirical research presented in Chapter 6 by focusing on how animals operate within their social environments, with particular emphasis on the prosocial behaviours that characterize strong social bonds between conspecifics. I review both the proximate and ultimate mechanisms that may explain spontaneous prosocial, or other-regarding behaviour, before reviewing the existing experimental studies on prosociality in nonhuman primates and providing directions for future research.

Chapter 4. Tool use and object exploration in the greater vasa parrot. This empirical chapter presents data on a novel form of spontaneous tool use in captive greater vasa parrots. Vasa parrots are also highly explorative birds, raising the question of whether exploration enables them to learn about physical properties of novel objects which can potentially be used as tools. I examined whether, when exploring novel objects, vasa parrots change their explorative behaviour to gain more information about objects that are structurally novel, and therefore behave differently.

Chapter 5. Function and flexibility of object exploration in kea and New Caledonian crows. This empirical chapter follows up the results of Chapter 4 by examining whether kea and New Caledonian crows can apply the information learned during their object exploration toward solving a task, and whether these birds change their exploration in order to learn about object properties once they have a task in mind.

Chapter 6. Prosocial behaviour in captive ravens. This empirical chapter examines the social cognitive abilities of corvids by measuring prosocial tendencies in ravens using a prosocial choice task in which birds can choose to donate food to affiliate or non-affiliate partners at little or no cost to themselves.

Chapter 7. General discussion. This chapter synthesizes the results from Chapters 4-6 to discuss how these studies contribute to our understanding of avian cognition, before providing directions for future research.

Chapter 2. Physical Cognition:
Tool Use, Problem Solving and Exploration

Animal tool use

Prior to Jane Goodall's first observations of tool use and manufacture by wild chimpanzees in the 1960s, tool use was historically assumed to be a defining characteristic of humanity. Indeed, when Goodall relayed these observations to her supervisor, Louis Leakey, he famously responded, "now we must redefine 'tool', redefine 'man', or accept chimpanzees as human" (Goodall 1998). In the 60 years following, increasing reports of tool use by nonhuman animals suggest that this behaviour is actually widespread across a range of taxa, from invertebrates to fish to mammals (reviewed in Beck 1980; Bentley-Condit & Smith 2010; Shumaker *et al.* 2011). Together these cases raise intriguing questions about the nature of tool use in other species, including how to define it, what it reveals about animal minds and ultimately what it means for the evolution of human cognition and technology.

Defining tool use

One of the first explicit definitions of tool use was proposed by Goodall herself, who broadly classified it as "the use of an external object as a functional extension of the mouth or beak, hand or claw, in the attainment of an immediate goal", which could be related to foraging, grooming or repulsion of intruders or predators (van Lawick-Goodall 1971, p195). In the years following, several other researchers have presented new or expanded definitions (Alcock 1972; Boswall 1977; Beck 1980; Pierce 1986; Bentley-Condit & Smith 2010), the most widely used among these being Beck's, which defines tool use as "the external use of an unattached environmental object to alter more efficiently the form, position or condition of another object, another organism, or the user itself when the user holds or carries the tool just prior to use" (Beck 1980, p10).

More recently, St Amant and Horton (2008) highlighted that aspects of this definition may be problematic, including the focus on manipulability of the object and alteration of the environment. For example, by Beck's definition, a monkey using a detached branch as an extension of the arm to obtain an out-of-reach fruit would qualify as tool use, however if the branch in question were still attached to the tree it would not. Similarly, if the branch were slightly too short to reach the fruit, the criteria of having "altered the environment" would not be met despite the fact that the apparent goal of the behaviour is to use the stick as a means to gain access to the fruit. St Amant and Horton (p1203) therefore propose a revised definition which would incorporate these alternative scenarios, and will be used throughout the remainder of this thesis:

> *"Tool use is the exertion of control over a freely manipulable external object (the tool) with the goal of (1) altering the physical properties of an object, substance, surface or medium…via a dynamic mechanical interaction, or (2) mediating the flow of information between the tool user and the environment or other organisms in the environment."*

In terms of cognitive ability, what classifies as true tool use is often less important than distinguishing between cases which might qualify as insightful or flexible problem solving as opposed to those which are more species-typical and inflexible (Seed & Byrne 2010). The following section reviews the existing cases for tool use in nonhuman animals, with a particular focus on two groups that exhibit some of the most flexible tool use known to date: birds and primates.

Tool use and tool manufacture in nonhuman animals

Tool use is incredibly rare in the animal kingdom, with roughly 1% of extant species documented as habitual tool users. Despite its rarity, however, cases of tool use are relatively widespread across taxa, with documented instances of tool use among invertebrates (Finn *et al.* 2009), fish (Brown 2012), aquatic mammals (Hall & Schaller 1964), birds (reviewed in Lefebvre *et al.* 2002) and primates (vanSchaik *et al.* 1996; Ottoni & Izar 2008; McGrew 2010) in a range of contexts including predator defence, foraging, and social displays (reviewed in Shumaker *et al.* 2011).

Some of the most frequent and sophisticated forms of tool use are found among nonhuman primates, with all great apes species (Nash 1982; Paquette 1992; Fontaine *et al.* 1995; Nakamichi 1999; Gold 2002; Nakamichi 2004) and several monkey species spontaneously using tools in captivity (e.g., pig-tailed macaques, Guinea baboons; Beck 1973, 1976). In the wild, however, habitual tool use occurs among only two great apes (chimpanzees and orangutans) and one New World monkey (tufted capuchins). Chimpanzees in particular feature an incredibly diverse and widespread tool repertoire, using tools for a range of different purposes including sticks to fish for termites, stones to open nuts and chewed up leaves to sponge water (McGrew 2010). In addition to their complex material culture, chimpanzees also manufacture tools, for example removing peripheral branches from a twig so that it may be inserted into the small opening of a termite's nest (McGrew 2010; McGrew 2013).

Wild orangutans also show relatively broad tool-using repertoires in the wild, however instances of tool use occur much less frequently than in chimpanzees (Meulman & van Schaik 2013). Most notably, populations of Sumatran orangutans manufacture and use stick tools to forage for insects or to extract seeds from the spiny *Neesia* fruit (vanSchaik *et al.* 1996). Among monkeys, capuchins are the only monkeys known to use tools regularly in the wild, with several of the more terrestrial, savannah dwelling populations using stone hammers to crack open encased nuts, fruits or seeds which they first position on stone anvils (Ottoni & Izar 2008). Additionally, several populations of bearded capuchins modify branches to use as probes when hunting for small prey or to dip for honey (Falótico & Ottoni 2014).

The frequency and complexity of primate tool use and tool manufacture has been rivalled only by the avian order, with several bird species making and/or using tools, primarily within foraging contexts. Populations of Egyptian vultures drop stones onto eggs in order to break them open (Van Lawick-Goodall & Van Lawick-Goodall 1966). In the Galapagos, woodpecker finches (one of the 15 species of Darwin's finches) use twigs and cactus spines to probe for arthropods within tree holes and crevices, often modifying tools beforehand by breaking off excess branches from twigs (Tebbich *et al.* 2002). Among birds, however, only one species is currently known to manufacture and use several different tools in foraging and non-foraging contexts in a manner comparable to chimpanzees (McGrew 2013). New Caledonian crows are an omnivorous corvid species endemic to the archipelago of New Caledonia. In the wild these birds manufacture stepped tools which are taken by stripping *Pandanus* leaves and orienting the barbs of the resulting petiole upward in order to extract grubs from holes in the bark. Like the chimpanzee, New Caledonian crows employ more than one tool by also manufacturing and using hooked twigs for a similar purpose (Hunt 1996). In addition to using tools in a foraging context, captive New Caledonian crows use stick tools to explore novel (and potentially threatening) objects (Wimpenny *et al.* 2011), thus meeting the criteria for flexibility.

Tool use and cognitive complexity

Human tool use has been proposed to play a role in the evolution of other uniquely human attributes including language and our sophisticated cognitive abilities (Nowell & Davidson 2010; Stout & Chaminade 2012). The complex nature of our own tool use often leads to the general assumption that tool use in other species reflects similarly complex cognitive functions. On the contrary, tool use encompasses a very broad category of behaviour that reflects a range of underlying cognitive substrates.

In general, tool-use behaviours are typically sorted into two categories depending largely on how flexibly they are employed within a species or individual (Call 2012; Biro *et al.* 2013). The first category refers to those behaviours which are innate within a species (stereotyped or hardwired behaviours). These behaviours are relatively inflexible and are usually restricted to one specific context. For example, California sea otters famously use stones as anvils to crack open oysters that have been gathered from the ocean floor, but they do not use stones in other contexts (e.g., to scratch themselves; Fujii *et al.* 2014). Such cases therefore represent behavioural specializations similar to the elongated finger of the aye aye (Sterling & McCreless 2006) or the beak of a woodpecker; and consequently may not require any sophisticated mental processes.

In contrast, flexible tool use (also known as creative tool use; Call 2012), represents a more varied category of behaviour, whereby the tool and its function are dissociated and the same tool can instead be used in multiple contexts. As previously mentioned, this is most evident among chimpanzees and orangutans in the wild, as well as New Caledonian crows (McGrew 2013). It is worth mentioning, however, that flexible and innate tool use are not mutually exclusive; for example New Caledonian crows begin manipulating stick tools after fledging and in the absence of conspecifics, but these skills can additionally be shaped by social influences (Kenward *et al.* 2006). In general, the wider tool-kits of chimpanzees, orangutans and New Caledonian crows suggest that the problem-solving abilities of these species are likely reliant on more general sensorimotor and/or conceptual abilities rather than context-specific actions triggered by specific stimuli, and consequently fall under the category of flexible tool use.

Evidence for the link between tool use and cognitive ability has been found in neuroanatomical studies of tool-using and non-tool-using species. After controlling for phylogeny and research effort, Reader and Laland (2002) found a significant positive association between tool use, behavioural innovation and both relative and absolute volume of the neocortex and striatum (two structures related to innovation and social learning) in primates. Similarly, Lefebvre *et al*. (2004) found significantly positive correlations between primate innovation rate, tool use and the size of the isocortex and striatum.

These same patterns were also found among birds, with corvids and parrots showing some of the highest frequencies of tool use. Lefebvre *et al*. (2004) used the same review methods to examine whether analogous structures within the avian brain correlate with reports of tool use or behavioural innovation, and found the same association between innovation, tool use and the size of the hyperstriatum ventrale and neostriatum, confirming earlier findings that tool-using species have a significantly larger residual brain size and residual neostriatum (Lefebvre *et al.* 2002). Additionally, the distribution of tool-using behaviour in birds suggested that it evolved multiple times within the avian order rather than through shared ancestry.

These findings lend support to the idea that tool use is a cognitively demanding yet beneficial way for some species to cope with their environments, as tool-using behaviour persists despite costly increases in the size of the brain or structures within it. However, this general relationship provides little information on how tool use operates at a species or individual level – what are the cognitive processes that underpin an animals' use of tools, and, in cases of flexible tool use, how did the behaviour originate?

Physical cognition in nonhuman animals

As briefly touched upon in the preceding section, behaviours such as tool use and object manipulation can serve as a window into the mind of the individual using the tool. Does the user understand what properties are required of a good tool, or how this particular item can function in a range of contexts? Given the way that various species can use and even manufacture tools it is often assumed that they possess some advanced understanding of the physical world relative to non-tool-using species. The aim of comparative psychologists is to test this assumption by conducting experiments to examine the physical cognitive abilities of tool and non-tool-using species; that is, how they use physical information to solve problems in their environments.

Understanding object properties

In the wild, tool-using species must choose from a range of potential objects that can function as tools, depending on the task they are faced with. When probing for grubs, for example, a long, thin tool will function better than a tool that is too wide or too short. The primary question among comparative psychologists is whether subjects choose these tools based on some abstract understanding of their functions, or whether preferences for particular objects have been developed through trial-and-error or social learning.

This question has been addressed with several controlled, captive tasks - focusing primarily on tool-using species – in which animals are presented with an array of tools, only some of which are suitable for the job. For example, Tebbich and Bshary (2004) presented tool-using woodpecker finches with a transparent tube with a reward inside, which was placed at various distances from the opening throughout the trials. In order to retrieve the reward, the birds had to choose a stick of equal or greater length. While all of the birds eventually learned to solve the task, they failed to choose sticks of adequate length from their first trial, and instead appeared to be using trial-and-error learning which eventually resulted in a preference for the longer stick tools.

Similar studies of tool selectivity have been conducted with New Caledonian crows. Hunt *et al.* (2006) examined the tools that two free-living crows manufactured and used to retrieve larvae from two different hole depths, and found that the birds initially produced tools of similar lengths for either shallow or deep holes, but after failing to retrieve food from the deep hole generally switched to making longer tools. In contrast, a later study featuring a larger sample size (N = 14 known individuals) found an association between the length of tools and the depth of the holes they were left in, suggesting that the birds were selecting tools based on their length, although whether this occurred spontaneously or through trial-and-error learning is unknown (Bluff *et al.* 2010). The former possibility has been demonstrated through captive experiments in which New Caledonian crows were found to preferentially choose tools that either matched or were longer than the distance needed to reach the food without a trial-and-error learning process, suggesting that these birds had formed some mental representation of the problem before attempting to solve it (note that sample size was small, N = 2; Chappell & Kacelnik 2002). When moving the location of the tools so that subjects had to leave the testing room to retrieve a tool, however, the one remaining subject made more errors than in the first condition, and switched to a strategy of choosing the longest tool. The performance on this second task relative to the first may be the result of the difficulty of coordinating mental representations of a goal and the tool being sought (Chappell & Kacelnik 2002). In a second study aimed at investigating whether New Caledonian crows select tools on another dimension of size (diameter) the one individual tested preferentially selected tools with the smallest diameter regardless of the size of the hole, even dismantling bundles of tools to select the thinnest among them. When allowed to manufacture tools to use in the same holes, both individuals tested made appropriately-sized tools on the majority of trials (Chappell & Kacelnik 2004).

In an earlier study, Visalberghi *et al.* (1995) presented chimpanzees, bonobos, capuchins and one orangutan with a baited, transparent tube and a set of tools which could be used to obtain the reward in the middle. The tools consisted of sticks tied together in a bundle or an H-shaped stick, both of which could be taken apart in order to use one of the pieces as a tool. Subjects from all species were able to solve the task, but apes in particular seemed to demonstrate some ability to plan their actions – for example, whereas capuchins frequently attempted to use the entire bundle of sticks as a tool (and appeared not to learn from these errors), apes never did so (Visalberghi *et al.* 1995).

In each of these cases, subjects were able to discriminate between these objects based on visual feedback, and so, rather than possessing some mental representation of which tool is suitable for the job (e.g., understanding that a particular minimum tool length is needed in order to cover the distance from the tube's opening to the reward), may have selected objects solely on the basis of their perceptual features (e.g., after being rewarded for using a longer tool on a trial, subjects may continue preferring longer tools without any understanding of why they are functional). Would they have done the same in the absence of obvious visual cues, for example when choosing among identical objects on the basis of hidden structural features such as weight, or by employing some understanding of cause-and-effect relationships?

Causal cognition

Humans' understanding of cause-and-effect relationships allows us to predict the outcomes of external events and, importantly, to intervene and control these events (Gopnik *et al.* 2004). For example, we know that cars stop at a red light, and by pressing a button, we can make the light red which causes the cars to stop and allows us to safely cross a road. Similarly, children as young as two are able to discriminate between several related objects to use only those objects which cause a box to light up (Gopnik & Sobel 2000).

The environments of nonhuman animals are similarly underpinned by causal structures (e.g., the wind causes a branch to move) and causal properties (e.g., objects are solid or heavy, and behave in predictable ways according to their properties; if an object is unsupported it will fall; Seed *et al.* 2011). The extent to which animals are aware of these contingencies has been a focus of research for decades, most notably using the trap-tube task (Visalberghi & Trinca 1989). In this task, subjects are presented with a clear horizontal tube with a food reward inside. On the bottom of the tube is a small trap. Subjects must use a stick tool to push the reward out of the correct end so that it does not pass over and fall into the trap. Individuals from an array of species have learned to solve this task, including orang-utans (Mulcahy & Call 2006), chimpanzees (Povinelli 2000; Martin-Ordas & Call 2009), gibbons (Cunningham *et al.* 2006), vervet monkeys (Santos *et al.* 2006), woodpecker finches (Tebbich & Bshary 2004; Teschke & Tebbich 2011) and New Caledonian crows (Taylor *et al.* 2009).

On the surface, success with this task would seem to imply some understanding of causal features of the task; namely that pushing the reward toward the trap will cause it to fall into the trap and be lost. Importantly, however, when the tube is inverted 180 degrees so that the trap is on top of the tube and no longer functional, subjects continue to avoid the trap, suggesting that their performance on the task was attributable to the use of a procedural rule (push from the end further from the reward) rather than an understanding of causality. It is also worth noting that even trial-and-error learning of such rules in the initial phase was a lengthy process, as many participants did not begin to reliably solve the task until around 100 trials (Povinelli 2000).

Though it continues to be used today, the trap-tube paradigm has since been reported as conceptually flawed, in particular because failure to ignore the trap in the inverted phase may not reflect an absence of causal knowledge (Silva *et al.* 2005). Instead, this continued avoidance may simply serve as a means to *guarantee* successful retrieval of the reward, as doing so in any case is not costly to the subject. Indeed, when running the same paradigm with adult humans, these participants, much like the nonhuman subjects, continued to avoid the non-functional trap in much the same way (Silva *et al.* 2005).

Additionally, though the initial phase of the paradigm was solved by subjects from a range of species, success rates were relatively low, so that typically only one to three of ten individuals would pass the first phase to then be tested with the non-functional trap (Povinelli 2000; Tebbich & Bshary 2004; Mulcahy & Call 2006; Tebbich *et al.* 2007; Taylor *et al.* 2009). Rather than lacking the problem-solving ability to pass the first stage of the task, the demands of the task may also have confounded performance. For example, when removing the necessity to use tools, Seed *et al.* found that 8/8 chimpanzees (2009b) and 7/8 rooks (2006) learned the correct method. Additional paradigms which remove the necessity of tool use but which still require the subject to use some understanding of physical or casual properties to solve the task yield similarly promising results (see Hanus and Call 2011 for an example).

Further evidence for potential causal reasoning has been reported from experimental studies of secondary, or meta-tool use, in which animals use an available tool (e.g., a short stick) in order to gain access to another, out-of-reach tool (e.g., a long stick), which may in turn be used to retrieve a food item (New Caledonian crows: Taylor *et al.* 2007; Wimpenny *et al.* 2009). In this case individuals with some causal understanding of the relationship between their species-typical tool use to extract food and this task, are expected to refrain from attempting to use the short, inappropriate tool to access the food, and to instead use it to retrieve the appropriate, longer tool. Remarkably, studies of New Caledonian crows reveal that subjects engage in spontaneous meta-tool use from their first trial (Taylor *et al.* 2007; Wimpenny *et al.* 2009). Although previous experience with the individual components of the task appears to facilitate success in these trials (Wimpenny *et al.* 2011), the overall results of both studies suggest that at least some individuals from this species may be solving this task using some causal understanding as well as potential planning (Taylor *et al.* 2007; Wimpenny *et al.* 2009). Importantly, Wimpenny *et al.* (2009) point out noticeable individual variation in strategies used to solve the task, highlighting the importance of considering individual differences in task performance, particularly with smaller sample sizes.

More recently, studies have shifted their focus from an understanding of causal structures to determine whether other animals are able to recognize the causal relevance of properties such as weight or rigidity in solving problems, with mixed results. While an early experiment by Povinelli (2000) suggested that chimpanzees fail to discriminate between rigid (functional) and flimsy (non-functional) tools to rake in a food reward, this was later contradicted by a study confirming that 9/9 chimpanzees solved an identical task (Furlong *et al.* 2008). This difference was attributed to the rearing history of the chimpanzees, as the chimpanzees in Furlong *et al.*’s study were highly enculturated, whereas the chimpanzees in Povinelli’s study were reared in comparatively impoverished environments with limited opportunity to develop their understanding of the physical world (Furlong *et al.* 2008, but see Manrique *et al.* 2010). Similarly, capuchins were able to select functionally appropriate, rigid tools to obtain an out-of-reach reward while ignoring irrelevant features such as colour and material, and did so from their first trial onward (Manrique *et al.* 2011). Correct tools were selected significantly more during conditions where subjects were able to physically explore the tools before using them or by observing an experimenter demonstrate the properties of the tools, supporting their conclusion that capuchin monkeys attend to the structural and functional properties of objects either through direct experience or observation.

These last few studies implicate sensitivity to the structural properties of the objects, but how do animals come to learn these properties? One possibility is that the unrewarded exploration of objects in the environment provides individuals with information that can later be applied to problem-solving tasks. The following section focuses on the role of exploration in learning about these properties.

Learning object properties: the role of exploration

In humans, the way that developing individuals begin to interact with different features of the external environment has long been accepted as playing a pivotal role in cognitive development, and in particular in developing more abstract concepts of object properties and means-end relationships that are critical to flexible tool use (Piaget 1952; Gibson 1988). This portion of the review focuses on the role that exploratory abilities might play in tool use and sophisticated problem-solving.

Object play or object exploration?

It is first important to address how different types of object manipulation are defined; within the literature, many researchers differentiate between object play and object exploration, usually with a focus on the underlying function of the behaviour. Object exploration is classically defined as an individual’s initial behaviour upon encountering a novel object (or environment), which allows them to gain information about unfamiliar stimuli (Weisler & McCall 1976). Exploratory behaviour would therefore feature more stereotyped, species-typical behaviours. In contrast, object play has been thought to be more intrinsically motivated, typically occurring in a relaxed environment that the individual is already familiar with (Hutt 1970). In short, whereas object exploration is generally stimulus-focused (‘what does the object do?’), object play is action-focused (‘what can I do with this object?’; Weisler & McCall 1976; Power 2000). It is important to note, however, that object exploration and play may extend beyond these contexts (e.g., individuals may play with novel objects or explore in familiar environments; Weisler & McCall 1976). Additionally, these terms may be difficult to separate in practice, as animals may rapidly switch between the two within one bout of manipulation (Weisler & McCall 1976). Given that both provide opportunities to acquire information about the physical world (Beck 1980), both terms are used interchangeably for the purposes of this review.

Exploration in children

At around 3 months of age, infants begin to explore objects and structures around them. From this point, the way they interact with objects continues to develop in both intensity and complexity until adolescence (Gibson 1988). The ontogeny of these manipulations has been classified most famously by Piaget (1952), who specifies five distinct stages of sensorimotor intelligence, the last three of which relate specifically to object exploration (outlined in Table 2). From around three to four months (before becoming mobile), infants begin engaging in secondary schemes by reaching and grasping nearby objects, and attempting to reproduce the effects of their actions on the objects (for example banging a wooden block on a hard surface, or shaking a rattle). At around 8 months, infants then begin embedding these secondary schemes hierarchically to distinguish between means and ends, for example by removing obstacles in the path of a goal (stage 4: coordination of secondary schemes). By one year of age infants begin creating relationships among two or more external objects to observe the effects of one object on another, in what Piaget calls tertiary schemes. These combined object manipulations, which allow individuals to appreciate causal relationships, may serve as the functional precursors of intelligent tool use.

Table 2. Piaget's first five stages of sensorimotor development in children.

Stage	**Type**	**Description**
Stage 1	Reflexes	Typically involuntary reactions such as sucking
Stage 2	Primary schemes	Directing exploration toward one’s own body
Stage 3	Secondary schemes	Intentional exploration of the external environment
Stage 4	Coordination of secondary schemes	Application of known means and ends, exhibited through hierarchical exploration of objects
Stage 5	Tertiary schemes	Relating objects toward one another

Exploration in nonhuman animals

While animals from a range of taxa rely on objects in their environment to some extent (e.g., in building nests, constructing shelters, etc.) the manipulation of objects outside of a functional context is less common, and found primarily among more generalist species (Napier and Napier 1985, Poirer and Smith 1974). These generalist species typically produce more altricial young which require longer developmental periods during which they can learn about their physical and social environments. For example, in a review of avian play, Ortega and Bekoff noted that altricial birds were more likely to engage in social and object play than species that produced precocial young (Ortega & Bekoff 1987).

In recent years, more systematic studies of object exploration and object play have documented these in a wide range of species including invertebrates (Mather & Anderson 1999; Kuba *et al.* 2006), fish (Burghardt *et al.* 2015), reptiles (Burghardt 2015), birds and mammals (Bekoff 2015; Janik 2015). Several early investigations of object manipulation in nonhuman primates attempted to categorize subject's exploratory behaviour within a Piagetan framework, and have revealed some informative differences. For example, macaques and spider monkeys will engage with artificial objects in their environment, but will not attempt to reproduce interesting effects or relate objects to one another (stage 3 of Piaget's sensorimotor scheme; Parker 1977; Antinucci *et al.* 1982; Chevalier-Skolnikoff 1989). In contrast, capuchin monkeys show a range of secondary and tertiary schemes with objects by relating objects to one another, reproducing interesting effects and manipulating objects hierarchically (stages 3-5; Parker & Gibson 1977; Chevalier-Skolnikoff 1989; Westergaard & Suomi 1994). Among apes, Vauclair and Bard (1993) found that humans infants performed the most tertiary actions with objects (12%), followed by chimpanzees (5%) and bonobos (0%).

Aside from primates, some of the most pronounced exploratory behaviour is found among birds, and corvids and parrots in particular. In an early review, Fagan (1981, p218) noted that "given the evolutionary opportunity, avian phylogeny can produce play like that of the kea, hyacinthine macaw, and common raven that appears to surpass most mammalian play in elaborateness and complexity". Captive kea, for example, readily explore and manipulate novel objects in captivity, exhibiting the final three stages of the Piagetan framework by frequently relating objects to one another, reproducing interesting effects and demonstrating means-end understanding (Gajdon *et al.* 2014). Another parrot species, the Goffin cockatoo, also shows pronounced exploratory behaviour characterized by combinatory actions similar to Stage 5 (Auersperg *et al.* 2015). Among corvids, juvenile crows and ravens show low levels of neophobia and high levels of exploration during development, and this behaviour changes depending on social context, with both species interacting with novel objects more frequently when conspecifics are present (Stöwe *et al.* 2006; Miller *et al.* 2015).

Personality and Exploration

In addition to these species-level differences, exploratory behaviour – whether object-focused or more general, such as exploration of the environment – also varies between individuals within a species, and these stable individual differences (often referred to as 'personality'; Reale *et al.* 2007) may have real consequences in terms of individual fitness (Dingemanse *et al.* 2004; Smith & Blumstein 2008). Animal personality features a number of traits but can generally be divided into five temperament categories: shyness-boldness, exploration-avoidance, activity, sociability and aggressiveness (Réale *et al.* 2007), which can be broadly related to the five general factors of human personality: neuroticism, agreeableness, extraversion, openness and conscientiousness (John 1990; Gosling & John 1999). In both human and nonhuman animals, these consistent individual differences predict how individuals respond to a range of novel or familiar situations and are thus important factors to consider in behavioural or cognitive tests (Gosling & John 1999; Réale *et al.* 2007).

One key personality trait that has been studied among nonhuman animals is exploration-avoidance, which is defined as an individual's response to a novel environment or object (Réale *et al.* 2007). Among birds, studies of species in the wild have shown that level of exploration is correlated with survival, but that this selection fluctuates across sexes and across years, thus allowing for individual variation in exploration levels to be maintained within the population. (Dingemanse *et al.* 2004; Smith & Blumstein 2008). Exploratory behaviour may also be influenced by context; for example, individuals born in captivity tend to demonstrate increased exploratory behaviour relative to wild individuals, as well as increased boldness and reduced neophobia (Yoerg & Shier 1997; McPhee 2003b, a; Benson-Amram *et al.* 2013). These factors have also been shown to relate to problem-solving ability, suggesting that setting is an important factor to consider when interpreting the results of cognitive or behavioural studies (Benson-Amram *et al.* 2013). For example, captive hyenas were more successful at accessing food in a novel puzzle box than wild hyenas as they were less neophobic and more explorative, showing a greater diversity of exploratory behaviours toward the box relative to wild hyenas (Benson-Amram *et al.* 2013).

Although it is not explicitly addressed by the research presented in this thesis, these studies highlight the importance of considering individual variation in behaviour, which may vary depending on context (e.g., wild or captivity) and may additionally predict performance in cognitive tasks, such that failure to perform on particular tasks may be attributable to non-cognitive factors such as neophobia (Benson-Amram *et al.* 2013). This has been illustrated by briefly examining one personality trait, exploration, but future cognitive studies would benefit from assessing the full range of an animal's temperament in order to determine which of these factors may influence performance, and how they may interact with one another (Carere & Locurto 2011; Griffin *et al.* 2015).

Overall, both the individual and species-level data show that there is wide variation throughout the animal kingdom in terms of which animals explore when, and how they structure their exploratory behaviour. One key question that remains unanswered from this data is, why?

Functions of play and object exploration

In contrast to other behaviours such as foraging or reproduction, mammalian play behaviour initially puzzled theorists as it appeared to have no immediate function. On the contrary, play behaviour - whether social play with conspecifics or asocial object play – bears high costs in terms of energy expenditure, time (that could be otherwise applied to feeding or mating) and increased predation risk as a result of increased conspicuousness or reduced vigilance. For example, young vervet monkeys suppress play behaviour during times of food scarcity (Lee 1984). Additionally, a study of predation on juvenile South American fur seals by Southern sea lions found that of 26 pups taken within the study period, 22 had been engaged in play behaviour immediately prior, and were apparently “oblivious to the other animals fleeing nearby” (Harcourt 1991, p510).

As Harcourt and others conclude, given these apparent survivorship costs, play behaviour in animals must confer extreme adaptive advantages in order to outweigh these costs. Indeed, it has now become apparent that similar to human development, play behaviour provides increased benefits in allowing individuals to develop skills required for survival in adulthood. In terms of object play, individuals may gain opportunities (either in ontogeny or adulthood) to acquire information about the properties of objects in their environment. Additionally, it allows them to practice motor skills necessary for food acquisition, including tool use. For example, from fledging, both woodpecker finches and New Caledonian crows begin manipulating tool materials and inserting them in crevices in the absence of prey (Tebbich *et al.* 2001; Kenward *et al.* 2006). Similarly, young chimpanzees begin exhibiting the precursors of tool-using behaviour from 0.5-3.5 years of age, for instance placing a nut on an anvil and hitting it with the hand, or just hitting a nut with a stone hammer without placing it on an anvil (Biro *et al.* 2006). Finally, object exploration may allow individuals to exhibit a range of novel behavioural sequences that may provide the basis for later tool use.

Some of the most compelling evidence for the link between tool use and object exploration comes from controlled comparative studies of exploration in tool-using and non-tool-using species. Young chimpanzees spend a significantly greater proportion of their time manipulating and playing with objects than young bonobos (Koops *et al.* 2015). Similarly, comparative studies of great apes and monkeys found that tool-using species generally spend a greater proportion of time manipulating tools (Parker 1974; Torigoe 1985). Finally, comparative studies with parrot and corvid orders have generally found that tool-using species demonstrate more frequent and complex object manipulation, and in particular combined object manipulation, than their closely related, but non-tool-using counterparts (Kenward *et al.* 2011; Auersperg *et al.* 2015).

‘Information hoarding’ and latent learning

As previously discussed, the prominent view for most of the 20th century within psychology was that nonhuman animals behaved primarily in terms of stimulus-response connections, in which animals modified their behaviour according to the strength of these connections, based on either positive or negative reinforcement (Tolman 1948). In a now-famous set of experiments, Tolman (1948) showed that learning could also occur in the absence of reinforcement, in what is termed ‘latent learning’ (Call 2012). In Tolman’s experiments, rats that were given an opportunity to explore a maze with no food present learned the routes faster than rats that had previous experience running through the maze to retrieve a reward at the end, suggesting that the unrewarded rats had formed ‘cognitive maps’ as they explored the maze.

To date, there are very few published studies aimed at systematically investigating whether other species learn from their experiences in the absence of direct reinforcement. This ability to acquire information through experience, however, could be considered crucial in a number of contexts, and is particularly relevant when considering cases of creative, or flexible tool use. In these cases, individuals with a propensity to explore objects would gain access to a major source of information which could later be applied to problem-solving contexts. This key assumption – that individuals are able to learn in unrewarded contexts – underlies most theoretical discussions regarding the function of object exploration, but has not been systematically addressed. This issue will be returned to in Chapter 5.

Summary

The literature reviewed thus far shows that a range of different taxa employ external objects in their environment as tools, and that tool use behaviours vary in terms of their flexibility, with tool use in some species reflecting an innate tendency, whereas other tool-using species employ tools more flexibly in a range of different contexts (Shumaker *et al.* 2011). Attempts to understand the cognitive underpinnings of tool use show that flexible tool users such as apes and New Caledonian crows are adept at selecting suitable tools based on visible properties such as size (Visalberghi *et al.* 1995; Chappell & Kacelnik 2002; Chappell & Kacelnik 2004), and there is further evidence to suggest that apes are able to solve physical problems based on causal reasoning or an understanding of abstract properties such as rigidity (Furlong *et al.* 2008; Manrique *et al.* 2010). This raises the question of how animals come to learn these properties. Among humans, object exploration plays a key role in cognitive development, providing individuals with opportunities to learn about physical properties and develop tool-using skills from a young age (Gibson 1988). Exploratory behaviour is also exhibited by species throughout the animal kingdom, with tool-using species in particular showing some of the most frequent and complex object play, either in ontogeny or as adults (Power 2000). Despite this link between tool use and object exploration, it is currently unknown whether individuals are actually learning about the functional properties of objects from exploration, and whether they explore objects with the goal of gaining this information. These two outstanding questions will be addressed in Chapters 4 and 5.

Although the studies presented in this chapter have dealt primarily with how animals solve physical problems, many of these studies also highlight the importance of social factors, for example through facilitating object exploration and shaping tool-using behaviour. As mentioned in Chapter 1, a species' social environment is one of the driving forces in cognitive evolution, and poses a unique set of challenges which also require flexible problem-solving skills. Chapter 3 turns its focus to how animals operate within their social environment and manage social bonds with other individuals through prosocial behaviours.

Chapter 3. Social cognition:
Prosocial Preferences in Nonhuman Animals

In addition to solving physical problems, all human and nonhuman animals face challenges in their social environment. Among socially complex species such as apes and corvids, animals benefit from the ability to keep track of constantly-changing relationships within and outside of their own social groups, and to use this information flexibly in order to procure food and mating opportunities (Byrne & Whiten 1989). Discussions of complex social cognition in nonhuman species typically emphasize that these abilities were selected for in a context of intense social competition in which individuals use social information in order to 'manipulate' or outcompete others for these fitness benefits (Gavrilets & Vose 2006).

In addition to these challenges, however, there are also myriad benefits to living in cohesive social groups characterized by strong social bonds. In humans, for example, the degree of social support an individual receives is correlated with physical and mental health (Thorsteinsson & James 1999; Cacioppo *et al.* 2000). Similar findings are accumulating for nonhuman species as well, including ravens (Stocker *et al.* 2016), dolphins (Frère *et al.* 2010) and baboons (Silk *et al.* 2003). Aside from investigating fitness benefits, there is a general wealth of evidence suggesting that nonhuman species form close social ties with group members, which are typically characterized by prosocial behaviours between partners including grooming, agonistic support and, less often, food sharing (Palombit *et al.* 1997; Jaeggi *et al.* 2010; Jaeggi & Van Schaik 2011; Kalbitz *et al.* 2016).

These behaviours and social relationships may serve as the foundation for cooperation within social groups (Silk & House 2011). In humans, cooperation takes an extreme and unprecedented form: we cooperate with other members of our species on a global scale, and often volunteer time and energy toward improving the welfare of people we've never even met (e.g., blood donation, disaster relief; Fehr & Fischbacher 2003). In recent years, understanding the evolutionary origins of our hyper-cooperation has become a key focus of animal cognition research, aimed primarily at determining whether the precursors of prosociality can be found in other species, and what drives these behaviours, both socially and psychologically

(Burkart & van Schaik 2010; de Waal & Suchak 2010; Cronin 2012; Burkart *et al.* 2014).

In both humans and nonhuman animals, prosocial behaviours are defined as actions which benefit another individual, regardless of the underlying intent of the actor (Dovidio *et al.* 2006). Whereas cooperation often involves coordination of behaviour between two or more individuals to achieve a goal (e.g., two individuals working to lift a heavy box to obtain food underneath; Stevens & Hauser 2004), prosocial behaviour, although closely related, focuses primarily on the behaviour of the actor (e.g., an individual obtains a piece of food and offers it to a group-mate; Silk 2007). A subset of prosocial behaviours can be further classified as altruistic behaviour, which is prosocial behaviour that occurs with no benefit (and in many cases a cost) to the actor (Schroeder & Graziano 2015). Thus, while all altruistic behaviours are prosocial, not all prosocial behaviours are altruistic. The extreme nature of our own prosociality has led some to propose that altruism is a hallmark of human evolution (Fehr & Fischbacher 2003), but in fact, altruistic behaviours can be observed in a range of species throughout the animal kingdom. These behaviours initially puzzled biologists as they appear to directly contradict the idea of natural selection and competition for survival – how could such costly behaviours persist if they increase the fitness of a recipient while decreasing the fitness of the actor? The next few sections address both the ultimate and proximate mechanisms that drive prosocial behaviour in nonhuman animals.

The evolution of prosocial behaviour

In terms of natural selection, prosocial and altruistic behaviours can only persist if they increase the inclusive fitness of the individual performing these behaviours (Brosnan & Bshary 2010). There is now widespread empirical support showing that prosocial behaviours may be ultimately explained in terms of the benefits they provide to the actor either directly (at a later time) or indirectly through the increased fitness of individuals sharing the actor's genes (Schroeder & Graziano 2015).

Alarm calling is one such behaviour that serves to warn conspecifics of nearby predators while simultaneously drawing attention to the caller, thus putting them at increased risk. Alarm calling behaviours may best explained in most species in terms of kin selection as they increase the inclusive fitness of the caller by conferring survival benefits to nearby, and often closely-related, conspecifics (Hamilton 1964; Axelrod & Hamilton 1981). Indeed, it has been shown that some animals, including female Belding's ground squirrels, alarm call more in the presence of closely related kin (Sherman 1977).

Altruistic acts among non-related individuals were originally less easily explained. Vampire bats, for example, often return to their roosts to provide food to individuals that failed to feed (Wilkinson 1988). In most cases these individuals were genetically unrelated to the donor, and instead the most common predictor of food transfer was whether the donor had previously received food from that individual (Carter & Wilkinson 2013). Although the evidence for reciprocal altruism among birds is scarce and often controversial (Koenig 1988), at least one species, the pied flycatcher, has demonstrated reciprocal altruism by selectively defending the nests of distant neighbours that had previously defended their own nests from a predator (Krama *et al.* 2012), or selectively assisting neighbours in predatory mobbing if those neighbours had previously assisted them (Krams *et al.* 2008). This supports the hypothesis that prosocial acts toward genetically unrelated individuals can be explained through reciprocal altruism, in which individuals incur costs in order to receive benefits at a later time (Trivers 1971).

Proximate explanations for prosocial behaviour

While kin selection and reciprocal altruism explain how prosocial behaviours can persist within a species, they do little to explain the immediate factors that prompt prosocial actions. Unless an individual's behaviour is immediately rewarded through short-term reciprocity, it is unlikely that they will associate their acts with benefits that are often indirectly linked (such as kin selection) or temporally separated (long-term reciprocity; de Waal & Suchak 2010). Instead, acts of prosociality may be explained in proximate terms as either proactive or reactive, resulting either from intrinsic motivation or external stimuli (Jaeggi *et al.* 2010).

Most of the prosocial acts observed in the animal kingdom occur in response to an external stimulus. Food sharing in primates, for example, occurs almost entirely in a passive context (i.e., tolerated theft) or in response to the begging signals of other individuals, and is rarely unsolicited (Jaeggi *et al.* 2010). Similarly, upon hearing the begging calls of pups, cooperatively breeding meerkat adults will respond by provisioning the pups. Importantly, however, when begging calls were broadcast from a speaker, adults continued to deliver food to the speakers indiscriminately (Madden *et al.* 2009). These behaviours thus do not require any internal motivation to benefit the welfare of others, and instead occur as relatively inflexible responses to extrinsic factors.

Proactive prosociality, which occurs in the absence of external cues and may therefore reflect an intrinsic motivation to aid others, is observed much less frequently in nature. One example of such behaviour occurs in cooperatively breeding callitrichid monkeys, which will proactively provision young by emitting specific calls to advertise food transfer to offspring. In these cases, the individual must suppress their own desire to eat the food in their possession, and may produce food-transfer calls more often when infants are out of sight (reviewed in Jaeggi *et al.* 2010).

These results show that prosocial behaviours exist in a range of species and can be biologically driven in a manner similar to parents' provisioning of their offspring, but further research is needed to determine whether i) prosocial behaviour exists across different contexts as it does in humans, ii) what factors prompt prosocial actions in different species and iii) how these behaviours were ultimately selected for. Within the last decade a surge of research has aimed at investigating prosociality in nonhuman species, typically from an anthropocentric viewpoint to determine whether human-like prosocial preferences are also present in other primates (e.g.,(Silk *et al.* 2005; Burkart *et al.* 2007; Vonk *et al.* 2008; Cronin *et al.* 2009; Cronin *et al.* 2010; Takimoto *et al.* 2010; Horner *et al.* 2011; Burkart & Van Schaik 2012; Burkart *et al.* 2014; Tan *et al.* 2015)). These studies are typically aimed at determining whether individuals will behave prosocially toward conspecifics in a novel context, and if so, what factors (e.g., partner identity, begging by the partner) prompt these actions. The results of these experiments are then incorporated into a broader evolutionary framework to determine what life history traits might predict which species behave prosocially toward conspecifics.

Measuring prosociality in nonhuman animals

The two most common tasks used to investigate prosociality in nonhuman species are the prosocial choice task (PCT; Silk *et al.* 2005) and the targeted helping task. In the prosocial choice task, a subject (also termed donor) is present in a testing compartment and may choose between one of two options: the first option delivers food to only the subject and the second option delivers food to the donor and a nearby conspecific, usually by pulling a tray, exchanging a token or pressing a button. If subjects are prosocially motivated, they are expected to preferentially choose the option that delivers a reward to both themselves and a recipient (commonly referred to as the 1/1, or prosocial, option) rather than the option that only delivers food to themselves (1/0, or selfish option). Payoffs to donor and recipient may also be manipulated to examine altruistic preferences (no payoffs to donor, only to recipient) or inequity aversion (unequal rewards distributed to donor and recipient).

In the targeted helping paradigm, subjects are paired with conspecifics that require their assistance in order to solve a problem (e.g., Warneken & Tomasello 2007). These scenarios usually involve retrieving an out of reach tool for a group member or human experimenter. If subjects in these instances are prosocial, they are expected to assist their partner when demonstrating signs or signals of need (as they are often in a separate room where they cannot see the task their partner is presented with) significantly more than the control condition in which the partner does not demonstrate any need of assistance. As a greater number of experiments have utilized the prosocial choice task, and subjects in targeted helping experiments are generally expected to respond only to direct requests from their partner, this review focuses primarily on the prosocial choice task (which is also used in Chapter 6) to examine evidence for prosociality in varying species.

Prosocial primates?

The prosocial choice task has now been presented to a wide range of primate species, with generally mixed results (summarized in Table 3). Among chimpanzees, the majority of studies report that subjects do not demonstrate any signs of proactive prosociality and instead choose equally between prosocial and selfish options when partners are both present or absent (Silk *et al.* 2005; Jensen *et al.* 2006; Vonk *et al.* 2008; Yamamoto & Tanaka 2010; but see Horner *et al.* 2011). Bonobos, which have demonstrated willingness to share food with strangers in other paradigms (Tan &

Hare 2013) also show no prosocial preferences in the standard prosocial choice task (Tan *et al.* 2015).

Among monkeys, capcuhins have demonstrated prosocial preferences by provisioning kin and familiar individuals significantly more than unfamiliar individuals (de Waal *et al.* 2008, but see Suchak & de Waal 2010 for prosocial choices for both familiar and unfamiliar individuals), as well as demonstrating sensitivity to the benefits they provided to recipients by preferentially donating high value food rewards to recipients in varying contexts (Lakshminarayanan & Santos 2008; Takimoto *et al.* 2010). Similar to the data from apes, however, these results are not consistent across all studies, as recent research reported that capuchins are not prosocial in a task where they may choose to provide food to their group members (Burkart & Van Schaik 2012; Drayton & Santos 2014). Macaques have also demonstrated prosocial preferences toward dominants when also receiving food for themselves which the authors suggest may be a strategy to gain future tolerance or support (Massen *et al.* 2011), but do not choose prosocially at a cost to themselves (Burkart & Van Schaik 2012; Sterck *et al.* 2015). Finally, tests of prosociality in callitrichid monkeys including marmosets and tamarins have shown that these species tend to choose outcomes which benefit conspecifics (Hauser *et al.* 2003; Burkart *et al.* 2007; Cronin *et al.* 2010, Mustoe *et al.* 2015; but see Cronin *et al.* 2009; Stevens 2010).

Table 3. General overview of studies using the prosocial choice task to examine prosocial preferences in primates, including whether subjects were classified as prosocial or not prosocial by the authors of the study. Cooperatively breeding callitrichid species are *italicized*.

Species	**Prosocial**	**Not Prosocial**
Chimpanzees	Horner *et al.* 2011	Silk *et al.* 2005 Jensen *et al.* 2006 Vonk *et al.* 2008 Yamamoto & Tanaka 2010
Bonobos		Tan *et al.* 2015
Capuchins	de Waal *et al.* 2008 Lakshminarayanan & Santos 2008 Suchak & de Waal 2010 Takimoto *et al.* 2010	Burkart & Van Schaik 2012 Drayton & Santos 2014

Macaques	Massen *et al.* 2011	Burkart & Van Schaik 2012 Sterck *et al.* 2015
Tamarins	Hauser *et al.* 2003 Cronin *et al.* 2010	Cronin *et al.* 2009 Stevens 2010
Marmosets	Burkart *et al.* 2007 Mustoe *et al.* 2015	

Cooperative breeding and the evolution of prosociality

Although the results from primate studies are generally mixed, the early positive results found among callitrichids and capuchins (Hauser *et al.* 2003; Burkart *et al.* 2007; de Waal *et al.* 2008) relative to chimpanzees (Silk *et al.* 2005) were initially explained in terms of breeding system. Among the primates, callitrichid monkeys (marmosets and tamarins) are distinguished by their cooperative breeding system. These monkeys live in social groups characterized by one or two breeding pairs and non-breeding helpers of both sexes that provide alloparental care, such as provisioning and infant carrying, to offspring produced by the breeding pair. Additionally, these species exhibit high levels of social tolerance with very low levels of aggression, and groups are characterized by strong social bonds, with adults cooperating to defend a territory (reviewed in Burkart *et al.* 2009). Although not classified as a cooperative breeder, capuchin monkeys have been proposed to have an ‘intermediate’ breeding system in which individuals exhibit cooperative behaviours including carrying and provisioning unrelated offspring as well as food sharing among adults (Fragaszy *et al.* 1997; Mitani & Watts 1997; Jaeggi & Van Schaik 2011). Humans, which indisputably show the greatest levels of prosociality, are also classified as cooperative breeders (Burkart 2011).

This loose association between breeding system and prosociality has been taken as support for the Cooperative Breeding Hypothesis, which suggests that a psychological predisposition for prosociality was selected for in cooperatively breeding species which frequently engage in altruistic behaviours such as allomaternal care (Burkart *et al.* 2009; Hrdy 2009). The Cooperative Breeding Hypothesis further states that the social biases observed in cooperatively breeding species such as increased social tolerance and responsiveness to others’ signals may have resulted in enhanced social cognitive abilities, such that cooperative breeding may have ultimately driven the evolution of complex cognition in cooperatively breeding species including humans (Burkart *et al.* 2009; Burkart & van Schaik 2010; Burkart 2011). The authors further suggest that in our own evolutionary history, these enhanced social cognitive abilities associated with cooperative breeding were then paired with the existing cognitive abilities of an ape-like common ancestor (which included physical cognitive abilities related to flexible tool use, as well as the precursors of theory of mind) to ultimately drive the evolution of uniquely human cognition. Some of the strongest support for the Cooperative Breeding Hypothesis comes from a recent comparative study of 15 primate species, in which subjects were allowed to pull one available lever in order to bring food within reach to the rest of the group (also known as the group-service paradigm). In this study the strongest predictor of prosocial tendency was the level of allomaternal care demonstrated by species (Burkart *et al.* 2014).

The Cooperative Breeding Hypothesis has gained substantial attention within the last few years and has been the focus of much theoretical debate (McAuliffe & Thornton 2015; Thornton & McAuliffe 2015; Burkart & van Schaik 2016). Critics of this hypothesis argue that there is no evidence that cooperatively breeding callitrichids demonstrate advanced socio-cognitive skills relative to non-cooperatively breeding primates, and that instead callitrichids show some of the lowest levels of general intelligence among primates (Reader *et al.* 2011; Thornton & McAuliffe 2015). Similarly, a comparison of brain size (which could be seen as a proxy for cognitive ability) between cooperative and non-cooperatively breeding avian species within the parvorder Corvida found that cooperative breeding was not correlated with brain size (Iwaniuk & Arnold 2004), a finding which has also been replicated in cichlid fishes (Reddon *et al.* 2016).

In terms of prosociality, it can be argued that there is no substantial evidence that callitrichids show greater levels of proactive prosociality in experimental settings relative to other primates, particularly as studies from all primate species seem to include both positive and negative results. Thus, while there is some support for the Cooperative Breeding Hypothesis (Burkart *et al.* 2014), it remains a topic of extensive debate.

Future directions for prosocial research

Despite its controversy, the Cooperative Breeding Hypothesis has inspired numerous additional studies of prosociality within primates. As previously highlighted, these studies have generally produced mixed results, which in part may be due to the use of different paradigms within and between species, preventing any direct comparisons from being made across primates in general. Additionally, many of these studies include methodological confounds which may result in either Type 1 or Type II errors; a point which will be addressed in detail in Chapter 6 (also reviewed in Tan *et al.* 2015 and Marshall-Pescini *et al.* 2016).

Based on these results, one alternative proposal to the Cooperative Breeding Hypothesis is that prosociality is instead unique to the primate lineage (de Waal & Suchak 2010), but both of these proposals are currently extremely limited by the fact that very little research has examined prosociality in non-primate species, including a formal test of the Cooperative Breeding Hypothesis outside of the primate order. The mixed results of primate studies also highlight two key issues, which are i) the need to carry out research using comparable methods to other studies in order to facilitate large scale comparisons, and ii) to test prosocial preferences in several contexts before making broad conclusions on the presence of prosocial tendencies in a species.

In summary, further studies of prosocial preference in non-primate species are clearly needed in order to test the assumptions of the Cooperative Breeding Hypothesis, and these should focus on both cooperatively breeding and non-cooperatively breeding species. When possible, such studies should ideally use paradigms that are comparable with previous research in order to enable broad comparisons of performance across species, but should additionally test subjects in several different contexts or with different paradigms before concluding whether a species is prosocial or not. Finally, several methodological changes should be made to the existing paradigms to allow for more rigorous tests of prosociality, where negative results cannot be a result of failing to understand the paradigm. Each of these points is addressed with the empirical data presented in Chapter 6.

Chapter 4. Tool Use and Object Exploration in the Greater Vasa Parrot

The tool use data from Study 1 in this chapter are featured in the following publication:

Lambert, M.L., Seed, A.M. & Slocombe, K.E.. (2015). A novel form of spontaneous tool use displayed by several captive greater vasa parrots. *Biology Letters.* 11: 20150861.

Abstract

Object exploration among animals has been found to be a fundamental precursor to tool use which may provide animals with increased opportunities to innovate novel foraging techniques and learn about the functional properties of objects which may be used as tools. Parrots are a highly explorative group of birds that are frequently cited for their sophisticated problem-solving abilities, but cases of habitual tool use among psittacines are scarce. Study 1 reports observational data documenting the first evidence of tool use by greater vasa parrots (*Coracopsis vasa*). Several members of a captive population spontaneously adopted a novel tool-using technique by using pebbles and date pits to either i) scrape on the inner surface of seashells, subsequently licking the resulting calcium powder from the tool, or ii) as a wedge to break off smaller pieces of the shell for ingestion. Tool use occurred most frequently just prior to the breeding season, during which time numerous instances of tool transfer were also documented. In a follow-up experiment (Study 2), the link between exploration and tool use was explored by investigating whether the birds attended to the structural affordances of objects during their exploration. The birds were given sets of categorically similar objects to explore (e.g., lengths of rope of identical size, shape and material). Each set consisted of a baseline object, followed by two visually novel (i.e., differently coloured) objects, one of which was also structurally different from the other two (e.g., had a stiff wire hidden in the middle). There was a significant difference in the quality of behaviour directed toward structurally novel objects, with birds spending a greater proportion of time engaged in behaviours that would provide them with information about the structural

properties of the objects. These observations provide new insights into the tool-using capabilities of parrots and highlight the greater vasa parrot as a species of interest for studies of physical cognition.

General introduction

One way that animals have learned to exploit new opportunities and solve physical problems within their environment is through the use of external objects as tools (Beck 1980; Shumaker *et al*. 2011). As reviewed in detail in Chapter 2, this behaviour is widespread across different animal taxa and reflects varying degrees of cognitive sophistication, from innate adaptations to more flexible application of tools within different contexts (Byrne 1995; Shettleworth 1998; Seed & Byrne 2010). One hypothesis for how animals may come to use tools and additionally learn about their physical environment is through unrewarded object exploration, which provides opportunities to hone manual skills and learn about the properties of objects which are not immediately visible, such as weight or ridigity (Power 2000). This would allow individuals to form an idea of how different objects behave and potentially develop more abstract concepts about these 'hidden' properties. It would thus be predicted that individuals are attending to the structural features of objects as they explore (Chappell *et al.* 2012); for example studies of infants show that subjects change their tactile exploration to gain information about novel and invisible properties of objects (e.g., Streri 2000). While there is research documenting the different exploratory behaviours used by animals toward different novel objects (e.g., Glickman and Sroges 1966), very few studies have focused directly on whether animals similarly attend to these structural properties during exploration (see Demery 2013 for an exception).

Parrots are an ideal taxon for investigating physical problem solving as they are large-brained, social birds which frequently explore and manipulate objects. Additionally, there are recent studies which suggest that some parrot species show high performance on physical cognitive tasks (e.g., Auersperg *et al.* 2013). Compared to other groups, however, instances of tool use among parrots are relatively rare, and our understanding of parrot cognition is still limited due to the small number of species investigated. This chapter presents new data on spontaneous tool use in the greater vasa parrot, a highly explorative species which has thus far been neglected in cognitive studies. In order to determine whether the vasa's exploration provides opportunities to learn about structural object properties and what properties they attend to during exploration, I followed up the tool use observations by presenting birds with sets of visually and structurally novel objects to explore.

Study 1: Observations of tool use

Introduction

In the fifty years following Jane Goodall's first observations of tool use in wild chimpanzees (Goodall 1964), a surge of data has revealed that tool use is in fact taxonomically widespread, occurring in a diverse array of species from invertebrates to mammals (reviewed in Beck 1980, Bentley-Condit & Smith 2010, Shumaker *et al.* 2011). Despite its range across taxa, however, tool use remains a rare phenomenon, documented in less than 1% of extant species, and many of these occurring as isolated instances in one individual (Bentley-Condit & Smith 2010). Habitual tool use, defined as the recurring use of tools by several members of a population (Whiten *et al.* 1999, 2001), is reported much more rarely, potentially as a result of cognitive, mechanical or anatomical constraints (Hunt *et al.* 2013).

Some of the most notable examples of nonhuman tool use are found in large-brained birds and primates, with New Caledonian crows and chimpanzees manufacturing and employing tools in a range of contexts (McGrew 2013). Parrots, another large-brained order, are frequently cited alongside corvids for their sophisticated problem-solving abilities (Emery & Clayton 2005; Emery 2006; Huber & Gajdon 2006); however cases of habitual tool use among psittacines are surprisingly scarce. Among over 300 parrot species, only hyacinth macaws and black palm cockatoos have been reported using tools habitually, with the former using leaves and small sticks as wedges to open nuts, and the latter using rocks and empty nutshells to drum on trees during social displays (Bertagnolio *et al.* 1994, as cited in Lefebvre *et al.* 2002; Borsari *et al.* 2005; Rowley 1997, as cited in Auersperg *et al.* 2014). More recently several Goffin cockatoos have shown competency for making and using stick tools to retrieve out-of-reach objects after observing a demonstrator, although it is unknown whether this behaviour persists outside of an experimental context (Auersperg *et al.* 2014b).

Descriptions of tool-using behaviour in new species add intriguing new pieces to this puzzle and help to broaden our understanding of the neuroanatomical, social and ecological predictors of tool use across the animal kingdom. Vasa parrots are endemic to Madagascar and the neighbouring Comoros Islands, where they have been geographically isolated since their split from all other members of the superfamily Psittacoidea ('true parrots') roughly 35 million years ago (Kundu *et al.* 2012). Consequently, vasas are unique among parrots in a numbers of ways. Unlike most parrots which form strong monogamous pair bonds, vasa parrots are highly promiscuous, characterized by a female dominated social system (Ekstrom *et al.* 2007) and exhibit a high degree of social tolerance which permits routine transfer of food between individuals either through theft, tolerated theft or active donations of food from one individual to another (Lambert, unpublished data collected consistently throughout ongoing focal observations). Among birds they are also unusual as they develop pronounced external genetalia during the breeding season and form copulatory ties similar to those of some social canids which can last up to one hour (Wilkinson & Birkhead 1995).

This study reports the first evidence of spontaneous tool use in a group of captive greater vasa parrots. Data on the frequency, duration and nature of tool use, as well as the frequency and nature of tool transfers between conspecifics, are presented.

Methods

Study Site

The following research took place at the Lincolnshire Wildlife Park, a licensed zoo and registered charity located in Lincolnshire, UK. The Lincolnshire Wildlife Park houses approximately 2,000 parrots representing over 100 species, most of which are rehomed pets.

Subjects and housing

Subjects were ten adult vasa parrots (M: 6, F: 4) ranging in age from 1 to >14 years. Eight of the birds were born and parent-reared in a zoo environment while the two oldest birds, UF and BW, are believed to be wild-caught. None of the birds involved in this study were ex-pets. All birds were identifiable either by individual leg rings or distinct physical markings. Some of the subjects may have been genetically related; however in the absence of existing data on these relationships it is not possible to determine which birds within the group are kin. Prior to this study the birds had only participated in a touch screen task and a string pulling task (Krasheninnikova 2014).

The birds were housed together in an aviary consisting of an outdoor (9 x 5 x 5m; Figure 1) and heated indoor section (2.4 x 4.9 x 2.4m), where feeds (30% seed, 70% fruit) were provided twice daily. Dates were sporadically incorporated into the diet, and the remaining pits were randomly scattered about the aviary floor such that all birds had access to them. The floor of the outdoor enclosure consisted of soil, cockle shells (a known source of calcium for birds and reptiles Brenninkmeijer *et al.* 1997), wood chippings and pebbles, as well as small twigs that had fallen from branches placed in the aviary. Aside from these objects, no other potential tools were available. Novel items were regularly placed in the aviary for enrichment.

During the study period the birds were given access to breeding boxes in the aviary and were allowed to breed. One female (BW) occupied one of the breeding boxes and laid 3 eggs, all of which hatched, and the chicks fledged in July 2013. As BW mated with several males (UF, WD, and JD), it is unknown which male sired the offspring.

Figure 1. The outdoor enclosure of the aviary, where all observations and experimental trials took place.

Data collection

Tool-using behaviour was primarily recorded during ongoing focal observations that took place between March and October 2013. Observational sessions were spread throughout the day between 08:00 and 19:00. All observations were filmed using a Panasonic SDR-H80 camera mounted to a tripod. During observations, all occurrences of tool use by any bird, focal or non-focal, were recorded such that the focal observation was paused and the tool-using bird became the focus of observation for the duration of the tool-using behaviour. To gain an understanding of individual variation in tool-using behaviour, including not using tools, any interaction with seashells without the use of a tool was also recorded.

Tool use and any other interaction with the shells took place exclusively on the floor of the aviary and were thus conspicuous behaviours, making it possible to record this accurately on an all-occurrence basis (Altmann 1974). Information recorded during tool-using bouts included the identity of the bird, the object used as the tool and any tool transfers between birds. Outside of focal observations, any occurrences of spontaneous tool use were video recorded *ad libitum.* A total of 16 bouts were recorded *ad libitum*.

Interactions with the shells were placed into four discrete categories. Instances of tool use were recorded as one discrete event until the bird dropped both items from the beak for more than five seconds or switched to a new behaviour.

> *Pebble-seashell*: Bird places pebble inside of seashell and either i) uses tongue to grind pebble against seashell (see Figure 2 for an example) or ii) uses as a wedge to break apart seashell.
>
> *Date pit-seashell*: Bird places date pit inside of seashell and either i) uses tongue to grind date pit against seashell or ii) uses as a wedge to break apart seashell.
>
> *Seashell-unknown*: Bird either i) has an object in mouth while holding seashell that cannot be identified or ii) it is unknown whether bird has object in mouth while holding seashell.
>
> *Seashell-no tool*: The bird has picked up a seashell with the beak and it is clear that there is no tool involved.

Figure 2. A video still of male greater vasa parrot holding a shell in the foot while using the tongue to scrape a pebble on the inner surface of the shell. The pebble is highlighted in grey for clarity.

Any tool transfers between birds were recorded, including the identity of the birds, the object transferred and the type of transfer. Transfers were considered successful if the recipient bird ended up in possession of the tool, and were coded as the following:

> *Protested theft*: receiver takes the item from the donor's beak, and the donor protests either through behaviour (e.g., foot raising or moving away) or vocalisation.
>
> *Tolerated theft:* receiver takes the item from the donor's beak and there are no signs of protest by the donor.
>
> *Active offer:* donor approaches receiver and allows receiver to take the item from their beak without any signs of protest.

Coding of behavioural data

All video recordings were coded in the Observer XT 10 to determine the duration that each bird spent engaged in each behaviour, as well as the type and frequency of tool transfers to other birds. As tool-using behaviour was not identified until the 18th observation session, all observations prior to this were retrospectively coded for any tool use that could be observed in the background of the video. The objects used as tools are relatively small and difficult to identify without close-up filming; consequently, of the 50 individual bouts extracted from these first 17 observations, 40 were coded as ‘seashell-unknown’ (seashell-pebble: N = 5, seashell-no tool: N = 5).

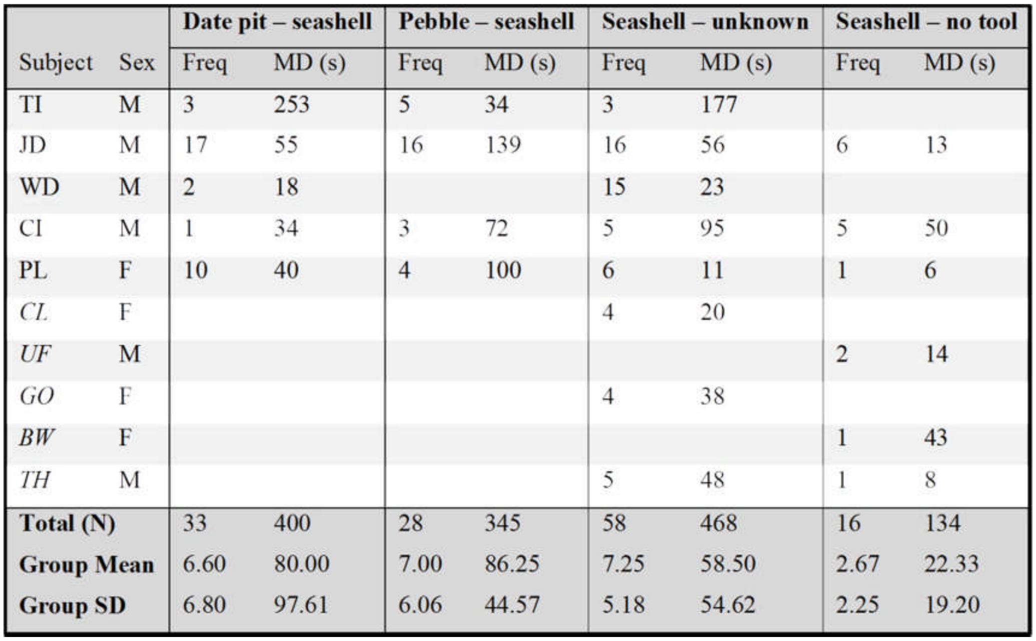
To ensure that the coding of the video recordings was accurate, an independent individual coded all categories of behaviour as listed in the methods section on a randomly chosen sample of 15 of the 135 bouts of interaction with the shells (11%). High levels of inter-observer reliability were obtained (Cohen’s kappa = 0.80).

Results

Tool-using behaviour was coded from a total of 107 hours of video observation data which included focal observations (105 hours) and ad libitum recordings (2 hours). Interest in the shells was greatest from March to mid-April 2013 (88% of tool-using bouts; mid-April to October: 12%). From April 2nd to April 11th, when data on shell interactions were coded on an all-occurrence basis, there were, on average 2.6 tool-using bouts in the group per hour (excluding cases of seashell-unknown).

Each individual’s total duration for using each of the different tool types is listed in Table 4. All ten birds were documented interacting with the seashells, and five of these birds were documented using tools, although this number is conservative as three additional birds in the ‘seashell-unknown’ category may have also been using tools. All five tool-using birds used date pits as tools, and four of these five individuals also used pebbles as tools on the seashells. The majority of confirmed tool-using birds (4/5) were male.

Table 4. All occurrences of recorded seashell interaction (tool use, no tool use or unknown). Table shows individual and group frequency for each of the behaviours, as well as mean bout duration (MD) of the observed behaviour at an individual and group level. Italicised subjects are those with no confirmed instances of tool use (only ‘seashell-unknown’ or ‘seashell-no tool’).



		Date pit – seashell		**Pebble – seashell**		**Seashell – unknown**		**Seashell – no tool**	
Subject	Sex	Freq	MD (s)	Freq	MD (s)	Freq	MD (s)	Freq	MD (s)
TI	M	3	253	5	34	3	177		
JD	M	17	55	16	139	16	56	6	13
WD	M	2	18			15	23		
CI	M	1	34	3	72	5	95	5	50
PL	F	10	40	4	100	6	11	1	6
CL	F					4	20		
UF	M							2	14
GO	F					4	38		
BW	F							1	43
TH	M					5	48	1	8
Total (N)		33	400	28	345	58	468	16	134
Group Mean		6.60	80.00	7.00	86.25	7.25	58.50	2.67	22.33
Group SD		6.80	97.61	6.06	44.57	5.18	54.62	2.25	19.20

Table 4 depicts clear individual variation in frequency of tool use with one bird, JD, emerging as the most prolific tool user both in terms of frequency and duration of tool use. The birds seemed to adopt qualitatively different strategies for using the objects on different occasions, in some instances picking up both the tool and the object in the beak and manipulating the tool with the tongue, while at other times holding the shell with the foot while using the beak and tongue to manipulate the tool. In in one bird’s (JD) case, tool use was extremely lateralized as he held the seashell in the left foot for 100% of occurrences. Another individual, CI, also used the left foot in 100% of occurrences, however this bird primarily held the shell in the beak and consequently there are too few (N = 4) cases of foot use to make any conclusions. Birds also appeared to have individual preferences for tool types, spending a greater portion of time using one particular object over the other. These preferences are tentative, however, as the greatest overall duration for seashell interactions fell into the ‘seashell-unknown’ category, so it is possible that the different tool types were being used in this category as well.

A total of 16 successful tool transfers took place and were exclusively from two tool-using males to the single tool-using female, PL. In 12 of these cases JD was the donor (date pit: 8, pebble: 4; tolerated theft: 11, theft: 1, active offer: 0), whereas WD was the donor in the remaining 4 cases (date pit: 4, tolerated theft: 3, theft: 0; active offer: 1).

Study 1 discussion

The greater vasa parrot joins the small minority of extant species documented as tool users. In addition, this bird's method of tool use appears to be entirely unique; a literature search of all cases of tool use among nonhuman animals yields no reports of any tool used for grinding (cases reviewed in Bentley-Condit & Smith 2010). The tool use observed appears to be flexible in several ways: firstly, individuals used more than one tool type on the shells; secondly, tools were used in different manners, to either grind or as a wedge to break off small pieces of shell and lastly, individuals were selective in when they engaged in tool use with this permanent feature of their environment in terms of season.

In the six month observation period, tool use was observed most frequently just prior to the breeding season from March to mid-April, after which point interaction with the shells – tool using or otherwise - became a rare occurrence. The concentration of tool-using events and overall interest in the shells just prior to breeding may be associated with the calcium requirements of egg production. Like eggshells, seashells are made almost entirely of calcium carbonate (Awang-Hazmi *et al.* 2007). Calcium supplementation prior to breeding season is critical for many passerine species, which are unable to store calcium in the skeleton (Pahl *et al.* 1997) and instead must increase their intake of calcium-rich foods such as snail shells or seashells prior to egg laying (Graveland *et al.* 1994; Brenninkmeijer *et al.* 1997). If a similar case exists for the vasa parrots, it is unclear why males appeared to show the greatest overall interest in the shells. During courtship, copulation and incubation, males feed females extensively through regurgitative feeding (Ekstrom *et al.* 2007), and thus it may be possible that the benefits of calcium ingestion are conferred to females indirectly, or that females actively prefer calcium rich regurgitation. Further longitudinal research is needed to first determine whether tool use and shell ingestion regularly occur primarily before each breeding season and if so, whether calcium intake is in any way related to breeding success.

The observations of tool transfer are particularly intriguing as it is rarely observed in other species and outside of mother-offspring dyads. Transfers occurred exclusively from males to females. This pattern is similar to that reported for chimpanzees, where females primarily received tools from males by means of tolerated theft, and in some cases females were in oestrus and transfer took place a short time before or after copulation (Pruetz & Lindshield 2012). The two males who transferred tools in the present study were the primary copulatory partners of the female recipient, however further data is needed to determine the various social factors that may influence tool transfer in this species.

Given the novelty of this behaviour both in this species and in general, there are a number of questions that remain unanswered. For instance, it is unknown whether vasa parrots interact with seashells or use tools in the wild, or whether this behaviour has arisen solely in this group, possibly as an artefact of captivity (e.g., lowered predation pressure and increased free time and energy; Haslam 2013). Additionally, as not all birds used tools on the seashells, the precise function of the tools requires further investigation. One possibility is that the use of a tool may mitigate discomfort from scraping the beak against the rough surface of the shell or prevent rapid wear of the beak. Alternatively it may increase foraging efficiency; for example, research within the poultry industry suggests that the particle size of calcium ingested from other molluscan shells affects absorption and retention of calcium both *in vitro* and in adult chickens, with small or ground particles being retained more efficiently than coarse particles (Guinotte *et al.* 1991; Guinotte *et al.* 1995). Dietary analyses are needed to determine the relative calcium intake of tool-using versus non-tool-using birds.

It is also unclear whether tool use in this population of birds reflects an innate predisposition, individual trial-and-error learning or some form of social learning. Whilst all five birds may have independently learned to use the tools on the seashells, the cases of tool transfer between individuals suggest that there is a social component to this behaviour, and therefore tool use may have been learned socially. The high social tolerance of these birds would certainly support social transmission of behaviour by allowing individuals greater opportunity to observe tool-using behaviour.

These data suggest a link between tool use and frequent and complex object exploration that characterises this species, but the precise nature of this link is largely unknown. Are birds gaining information about the functional affordances of potential tools through exploration? Study 2 examines whether object exploration in these birds serves as a route to tool using by determining what object features these birds attend to during their exploration.

Study 2: Novel object exploration

Introduction

Behaviours such as tool use and object manipulation can serve as a window into the mind of the individual using the tool. Does the user understand what properties are required of a good tool, or how this particular item can function in a range of contexts? Given the way that various species can use and even manufacture tools it is often assumed that they possess some advanced understanding of the physical world relative to non-tool-using species, however the cognitive processes that underlie tool use may vary widely between animals and therefore need to be empirically tested on a species-by-species basis (Seed & Byrne 2010).

As discussed in Chapter 2, one aspect of the more sophisticated physical cognition that governs creative and flexible tool use is the ability to distinguish between different objects on the basis of less obvious (or even invisible) physical properties such as weight or rigidity. Unrewarded, haptic exploration is an important means by which individuals can gain experience with these properties to then potentially apply in foraging contexts. The way that an individual manipulates and explores different objects can therefore provide insight into how they perceive and learn about their physical world, and which of its features they attend to or find particularly salient (Piaget 1952).

In humans, it is widely believed that the information gained during the period of intensive haptic, or tactile exploration in an infant's first couple of years has enormous cognitive consequences in allowing them to acquire knowledge about the world (Gibson 1988). Consequently, haptic exploration in humans has been a focus of developmental research since the 1930s in order to understand how our own mastery of the physical world, and indeed our cognitive processes in general, develop (Power 2000). These developmental studies can serve as useful tools, not only for comparing human and nonhuman cognitive abilities but also as a resource for designing methodology. Developmental researchers working with neonates and preverbal infants often face similar challenges to comparative cognition researchers in having to devise experimental protocols that investigate phenomenon in nonverbal subjects to whom they cannot provide specific task instructions. Whereas studies of cognition in non-primate species are relatively new, developmental research has had decades to refine and test the validity of its methods.

One of the most commonly used paradigms to determine what properties of objects infants attend to, and what motivates their exploration is the habituation/dishabituation paradigm (Kavšek & Bornstein 2010), where subjects are presented with novel objects to explore, and after becoming habituated to the object – as evidenced by a decrease in interest with each presentation – are presented with a novel object differing in some visual or tactile property. If the infants respond to the novelty of the object, this should be evidenced by some change in behaviour (e.g., looking or holding time).

Remarkably, this paradigm has been used to show that infants respond to changes in the structural properties of objects as early as 16 hours after birth. After presenting new-borns with an object to hold (e.g., a prism), behind a screen so that the object was not visible, Streri and colleagues (2000) observed the predicted decrease in holding time with each presentation. The experimenters then presented the subjects with a new item (e.g., a cylinder), after which they observed an increase in holding time, suggesting that infants were able to discriminate between these two structures based on haptic feedback alone. Similar results have been found among four-month-olds in detecting differences in objects based on their rigidity (Streri & Spelke 1988) and weight (Steri 1994, as cited in Streri 2003), again without any visual feedback.

As infants develop they then begin to refine their exploration in order to gain specific information about the novel property. For example, when presented with objects that have changed only in texture, infants spend a greater amount of time softly rubbing the hand over the top of the object, whereas when presented with objects that differ in shape, spend more time transferring the objects between hands or mouthing them (Ruff *et al.* 1984). In these cases, differentiation of exploratory methods based on object properties allows the infants to maximize the amount of information they can acquire about these changes (Steele & Pederson 1977).

Although there is a relatively large body of work on exploratory behaviour of nonhuman animals (as discussed in Chapter 2), there is very little data on whether nonhuman animals similarly attend to small changes in object properties, and if so, whether they change their behaviour in order to maximise the information available to them concerning these changes (Chappell *et al.* 2012). This question has been most explicitly addressed by Demery (2013), who used a similar habituation/dishabituation paradigm with kakarikis, a highly explorative parakeet species from New Zealand. Subjects were presented with a pair of objects to explore – a novel red ball and a familiar red rope – for three days. On the fourth day, the red ball was replaced with an object that differed either in colour, shape, or structure. Subjects showed the greatest increase in exploration when presented with an object that was visually identical to the red ball, but a ball bearing inserted in the middle meant that it differed in structure, or the way it behaved when manipulated. Similarly, a second experiment with the same birds showed that these concepts may generalize to novel objects; for example, when presented with novel objects that were symmetrical or asymmetrical in shape, birds spent longer exploring objects that featured an unexpected centre of gravity based on their symmetry, for example when symmetrical objects were weighted more on one side, or when asymmetrical objects had a balanced centre of gravity (Demery 2013). This result suggests that, like infants, subjects formed (potentially abstract) expectations of how objects behaved through manipulation and attended to structural changes that violated these expectations. Furthermore, individuals responded to these changes by increasing their explorative diversity to potentially gain new information.

Another exception is a study by Povinelli and Dunphy-Lelii (2001) which was aimed at investigating whether, upon encountering objects that behaved differently from their previously established expectations, chimpanzees and 6-year-old children would attempt to seek explanations for the object's change in behaviour, either through visual or tactile exploration. Specifically, subjects were trained/told to stand blocks upright for a reward, but some of these blocks were covertly manipulated so that they were near impossible to stand up. In the first condition, wooden, rectangular blocks were used, and one in four of these blocks had slightly bevelled edges so that they would not remain upright. In the second condition, subjects were required to stand inverted, L-shaped blocks at the top of their long end (so that the 90^o angle was at the top), some of which featured a hidden counterweight so that they would fall over. In both conditions, both the children and chimpanzees spent more than half of the allotted trial time (120s) attempting to stand the manipulated objects. Crucially, however, the chimpanzees only performed visual and/or tactile investigations of the faulty objects in the first condition when the objects were not visually identical due to the bevelled edges, suggesting the increased interest may have been due to the objects' perceptual novelty. In contrast, the children investigated the faulty blocks in both conditions, in many instances looking at the bottom of the block and asking questions such as "why" after the block failed to stand.

This key difference between the studies suggests that the chimpanzees are quite attuned to slight perceptual differences in stimuli, but do not attend to or try to seek explanations for structural differences influencing the way an object behaves, whereas children do so from as young as three years old. Notably, however, the same chimpanzees were featured in both studies, whereas different groups of children were used between studies. Additionally, rather than simply focusing on exploration as the infant and kakariki studies did, the chimpanzees had been trained to use the blocks as a means to an end which could have diverted their attention from these more subtle properties as they persisted in trying to achieve their goal by repeating the actions they had previously been rewarded for.

Further data using paradigms similar to those used with infants and kakarikis are a promising avenue for investigating the factors that influence exploration in other species as they are easily adapted to other species, feature low cognitive demands and do not require any training beforehand. As work on both of these species has shown, despite their apparent simplicity these methods allow us to gather important data on a subjects' perception of the physical world by simply capitalizing on a pre-existing, intrinsic motivation to explore its environment.

This study features an adapted novel response paradigm similar to the infant and kakariki studies described above to determine if, when presented with objects that differ structurally, vasa parrots change the duration or quality of exploration toward these objects more than objects that differ only perceptually (i.e., in colour). In this paradigm, subjects are presented with a baseline object to explore over several days so that they are habituated to its properties. Following this, subjects are then presented with two further object types for matched periods, both of which are perceptually novel to the birds (e.g., different colours), but one of which is also structurally novel. If birds are attending to the structural properties of objects as they explore them, they are expected to either increase or change their exploration of the structurally novel object relative to the baseline object. In contrast, if exploration is driven by visual novelty, birds are expected to explore all objects equally.

Methods

Objects

The group was presented with three sets of novel objects (stuffed socks, ropes and canisters; Figure 3) to explore in their aviary. Each set consisted of three categorically similar objects, with each of these objects presented sequentially, such that only one object type was available for exploration at a time. All of these objects were perceptually novel (i.e., differently coloured), and one of which was also structurally novel. For example, the rope set consisted of three differently coloured lengths of rope, all of which were identical in size, shape and material (Figure 3), but one of which had a wire inserted in the middle and was therefore structurally different from the other two ropes.

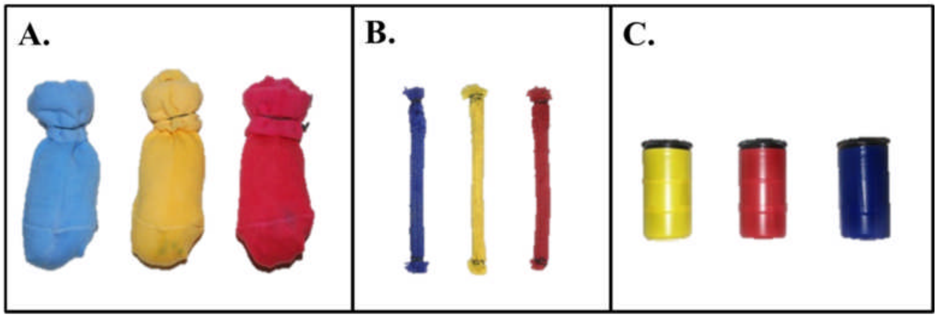


Figure 3. Object sets. 2A) socks; 2B) rope; 2C) canisters.

Each object set featured one red, one yellow and one blue object, and the colour of the structurally novel object was different in each set. These different colours were used to increase the chance that subjects would approach and explore all of the objects due to their novel appearance. The baseline objects (the first object presented in each set) provided a baseline measure of each bird's interaction with a novel object, which could then be compared to their rate of exploration for either the perceptually novel object (i.e., the object that was a different colour, but same structure as the baseline object) or the perceptually and structurally novel object (i.e., the object that behaved differently from the baseline object) to determine whether any change in exploration was due to structural or perceptual novelty alone.

A total of three object sets were presented to the birds. The first object set, socks, was used as a pilot set (Figure 3a). This set included two socks that were filled with cotton-wool (one yellow and one blue) and were soft when pressure was applied to them. The structurally novel item in this set was a red sock filled with aluminium foil that was hard and crunchy by comparison when pressure was applied. This pilot set was used to determine how to best present the objects and for how long to maximize the chances of each bird interacting with all of the objects within a set. Because the pattern of presentation for the pilot set was slightly different, it was not included in the combined data analysis.

The rope set featured three different ropes, each of which was 17cm long and 0.75cm in diameter (Figure 3b). The yellow, structurally novel rope had a wire inside so that it remained stiff when picked up. The third object set consisted of three different film canisters (Figure 3c), all weighing 30.2 grams, and one of which contained magnets and therefore showed some resistance when being picked up off of the metal fence. Each canister was additionally filled with cotton-wool so that no sounds were made when the object moved.

Presentation of object sets

Object presentations took place from September to November 2013. Each object in a set was presented individually for four consecutive days, for a total of 6.2 hours per object, in order to ensure that, similar to developmental studies, subjects would likely have habituated to these objects prior to encountering the next object type. To control for order effects, the presentation order of the structurally novel object was counterbalanced between second and third, such that subjects were always presented with an baseline object for the first four days, which was then followed by either a structurally novel object for days 5-8 and a perceptually novel object for days 9-12, or vice versa. To avoid any potential colour biases, the colour of objects was also counterbalanced across objects sets as much as possible, although priority was given to counterbalancing the colour of structurally novel objects (see

Table **5**). Although efforts were made to ensure that the objects presented were truly novel, it is difficult to rule out that the birds may have had experience with similar objects within their lifetime. As this study focuses on the differences between objects within a set, this is not predicted to affect the results.

In order to prevent objects from being monopolized by one bird, two copies of each object were presented. The objects were hung on the fence inside of the aviary 45cm apart from each other, and could not be removed from the fence. A target zone was clearly marked around the objects so that subjects were in the target zone if they were anywhere on the fence within 30cm of the objects. The area of the target zone was 1.2 x 1.3m. As vasa parrots show high levels of attraction toward shiny metal objects, the objects were hung from key rings, and the same key rings were used for all object sets. As additional incentive for all birds to enter the target zone to interact with the objects, small amounts of palm oil butter were smeared on the fence behind the object at specified intervals that were kept identical for all objects within a set. As data from the pilot set showed relatively low levels of engagement by some individuals, these measures were taken to increase the likelihood that multiple birds from the group would engage with all objects within a set.

Table 5. Order of object presentation for each set. Structurally novel objects are bold. Note that 'days' are counted as experimental days, although there was a minimum of one day in between presenting each object, depending on the set. The socks set, which was used as a pilot set and is not included in the analyses, is italicized.

Set	Object 1 **Days 1-4**	Object 2 **Days 5-8**	Object 3 **Days 9-12**
Socks (pilot)	*Yellow*	*Blue*	***Red***
Rope	Blue	**Yellow**	Red
Canisters	Yellow	Red	**Blue**

The overall pattern of presentation was also kept identical within object sets, so that all objects within a set were presented at exactly the same time of day. Trials took place either between 9am and 11am or 1pm and 3pm, immediately preceding either the morning or afternoon feeding. The pattern of presentation between sets was also similar in that each object within a set was presented in the morning for three of the four days of presentation, and in the afternoon for one of the four days. As the birds generally showed low activity levels during rainy weather (Lambert, personal observation), objects were never presented when raining. If weather prevented a trial from taking place, the trial was rescheduled for as soon as possible on that same day. This happened once on the fourth day of red rope presentation so that presentation took place at 1pm rather than 9am. There was one non-experimental day between each rope object presentation, such that birds encountered object 1 during days 1-4, then object 2 during days 6-9, and finally object 3 during days 11-14. Due to practical limitations there were three non-experimental days between canister presentations, so that birds encountered object 1 during days 1-4, then object 2 during days 8-11, and finally object 3 during days 15-18. As this study focused on exploratory differences within the sets rather than between, this is not predicted to influence the results as the pattern of presentation was still kept identical for all of the items within a set.

Behavioural data

All trials were filmed from outside of the aviary while the experimenter commentated the identities of birds in the target zone as well as their interactions with the objects. All trials were coded using Observer XT 10. The amount of time that birds spent in the target zone was recorded, as well as all behaviours directed at the objects, including biting, picking up with the beak or foot, and touching with the beak, foot or tongue (see Table 6). Because not all birds spent the same amount of time in the target zone and could be displaced by dominant individuals, all behaviours were recorded as a proportion of time spent within the target zone.

Table 6. Full ethogram for all behaviours directed at the objects.

Behaviour	**Definition**
Inside target zone	Parrot is on fence inside of specified target zone
Displace bird from object	Parrot causes another bird to leave object, either through approach or direct aggression (e.g., pecking)

Contact metal	Parrot uses beak to interact with metal keyrings attaching object to fence
Tongue touch	Parrot touches object with the tongue
Touch with foot	Parrot touches the object (excluding the metal keyring) with its foot. Considered one discrete bout until the bird places the foot on another surface.
Touch with beak	Parrot touches the object with the underside of the maxilla which generally hangs over the mandible when the beak is closed. This does not include touching with the outer part of the beak, particularly when nudging the object aside to get palm oil
Pick up with foot	Parrot picks up the object with foot so that either part (rope) or all of the object is no longer in contact with the fence (rope and canister)
Pick up with beak	Parrot picks up the object with beak so that either part or all of the object is no longer in contact with the fence
Bite	Parrot grabs object with upper and lower beak without removing from the fence

In addition to examining any differences in the proportion of time spent exploring objects, I was also interested in identifying any differences in the quality of exploration with the different object types (baseline, perceptually novel or structurally and perceptually novel). Two different categories of behaviour were considered: the ‘exploratory behaviour’ category included all behaviours directed at the objects, and a subset of these behaviours were also placed in the ‘relevant behaviour’ category, which included those behaviours which would have allowed the bird to actually experience the structural properties of the object (e.g., picking up or biting a rope to determine whether the rope was stiff or floppy; see Table 7).

Table 7. Exploratory behaviours coded from the videos. Relevant behaviours are a subset of exploratory behaviours that allow subjects to experience an object’s structural properties (e.g., picking up or biting a rope). Relevant behaviours for rope are bold, and for canisters are marked with an asterisk*.

All exploratory behaviours
Touch with tongue
Touch with beak
Touch with foot (modifier: which foot)
Pick up with beak *
Pick up with foot (modifier: which foot) *
Bite

Previous experiments on novel object presentation with rodents have shown the greatest increase in exploration during the first moments of encountering a novel object (Ennaceur 2010). To determine whether birds showed the greatest interest in novel objects during their first encounter, each bird’s exploratory behaviour within the first 15 seconds of experiencing an object’s structural properties, meaning the first 15 seconds after first performing a relevant action, was also examined. As no birds were displaced during their first 15 seconds, the raw times were used.

Analyses

All data were analysed using SPSS 21. Data from birds that interacted with all items within a set were analysed (both sets: N = 4, rope only: N = 2, canisters only: N = 1). These data were then combined (N = 7) and scores were averaged for individuals (N = 4) that were included in both sets. Due to the small number of individuals that interacted with the objects, nonparametric, two-tailed tests were used, and all results reported are for the combined data. A Friedman’s test was used to determine whether colour biases may have affected the amount of time birds spent interacting with the objects.

Planned comparisons were used (Wilcoxon signed-rank tests) to investigate the difference between exploration of i) baseline and perceptually novel objects, and ii) baseline and structurally novel objects. It was predicted that if birds were attending to the structural novelty of objects, there should be a significant increase or change in exploration between baseline and structurally novel objects, but not between baseline and perceptually novel objects. For all paired comparisons, effect sizes were calculated using Pearson's *r* (Fields 2009, p558).

Results

For both the canister and rope sets, subjects spent an average of 19.5% of trial time in the target zone near the objects (ropes: 2 - 55%, S.E. 8%, for individual birds; canisters: 0.5 - 41%, S.E. 7%, for individual birds; Figure 4). For the canister set, birds spent an average of 27% of this time interacting with the objects (range: 3 - 68%, S.E. 12%), and for the rope set they spent an average of 23% of their time in the target zone exploring the objects (range: 2 - 49%, S.E. 7%). Figure 5 shows the average amount of time that each bird spent exploring the objects on each day of presentation (both object sets grouped).

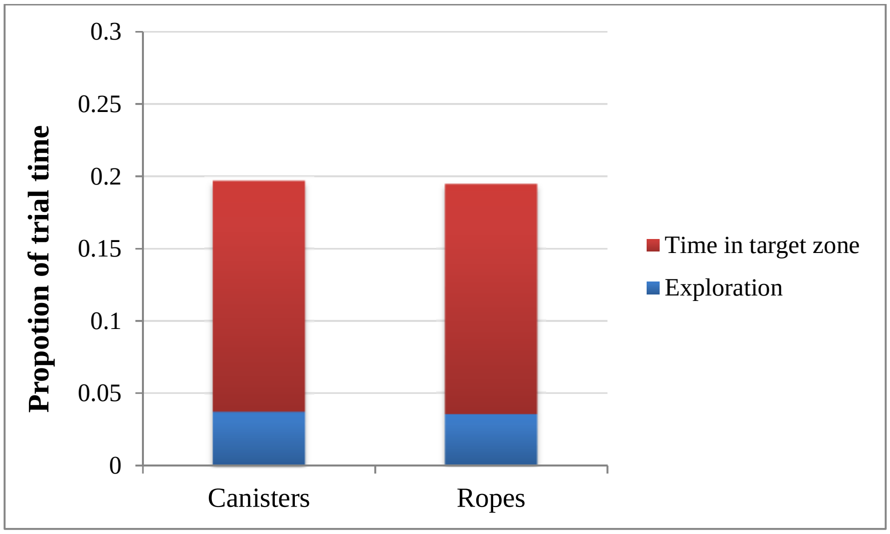


Figure 4. Average proportion of trial time that subjects spent in the target zone for each set, and average proportion of time within the target zone spent exploring the objects.

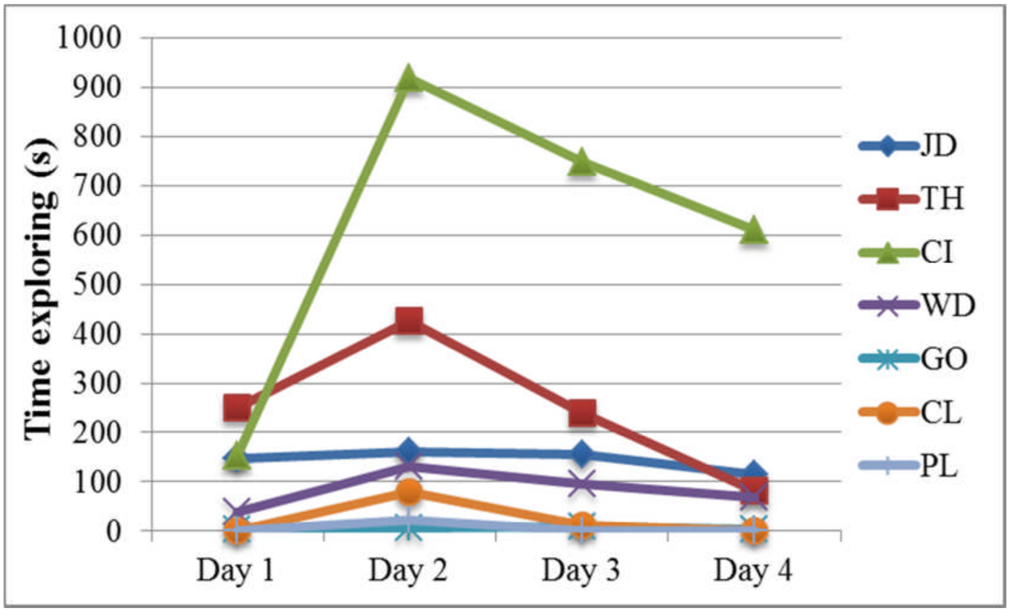


Figure 5. Each bird's average amount of time spent exploring the objects on Days 1-4 of presentation. Day averages are for all objects (baseline, structurally novel and perceptually novel) in both the ropes and canister set (6 data points per day per individual).

When the combined data from ropes and canister sets were analysed, there was no significant difference in the proportion of time in the target zone that birds spent exploring baseline vs. perceptually novel objects (Z = -1.014, N = 7, *p* = 0.375, *r* = 0.27), or baseline vs. structurally novel objects (Z = -1.014, N = 7, *p* = 0.375, *r* = 0.27; Figure 6). Similarly, there was no significant difference in the proportion of time that birds spent engaged in relevant behaviours when exploring baseline versus perceptually novel objects (Z = -1.859, N = 7, *p* = 0. 078, *r* = 0.49). However, the birds spent a significantly greater proportion of time engaged in relevant behaviours when exploring structurally novel objects relative to baseline objects (Z = -2.028, *p* = 0.047, *r* = 0.54; Figure 7).

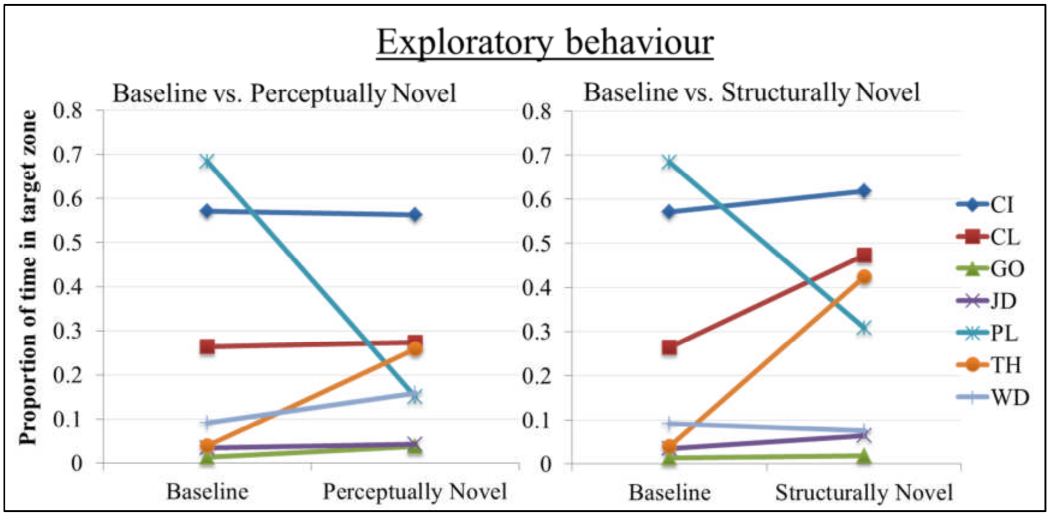


Figure 6. Proportion of time within target zone that each bird spent interacting with baseline versus perceptually novel objects, or baseline versus structurally novel objects. Data are from canister and rope sets combined.

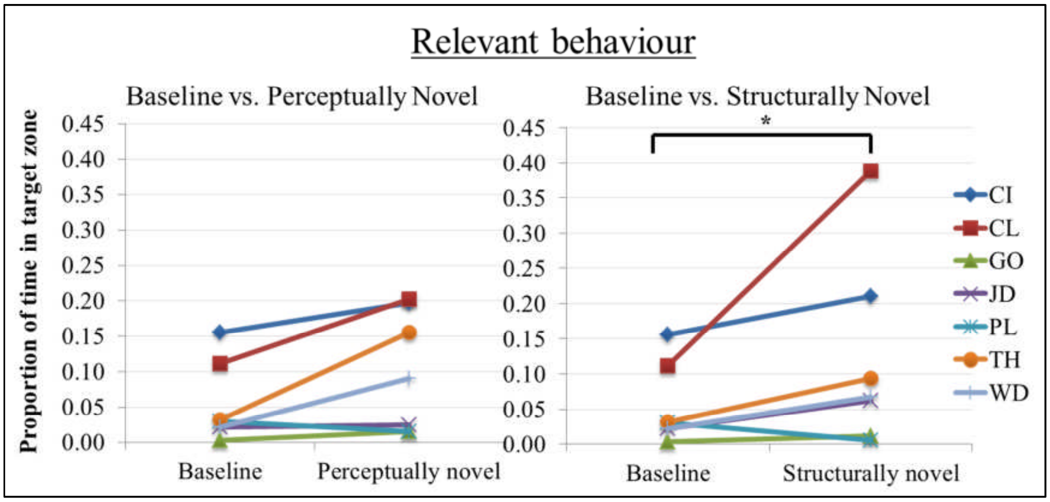


Figure 7. Proportion of time within target zone that each bird spent engaging in relevant behaviours for baseline versus perceptually novel objects, or baseline versus structurally novel objects. Data are from canister and rope sets combined.

There were no significant differences in time spent interacting with the different object types in the 15s after performing a relevant behaviour, either for all exploratory behaviours (baseline vs. perceptually novel: Z = -0.845, N = 7, *p* = 0.469, *r* = 0.23; baseline vs. structurally novel: Z = -1.183, N = 7, *p* = 0.297, *r* = 0.32; Figure 8) or for relevant behaviours (baseline vs. perceptually novel: Z = 0, N

= 7, *p* = 1, *r* = 0; baseline vs. structurally novel: Z = -0.676, N = 7, *p* = 0.578, *r* = 0.18; Figure 9).

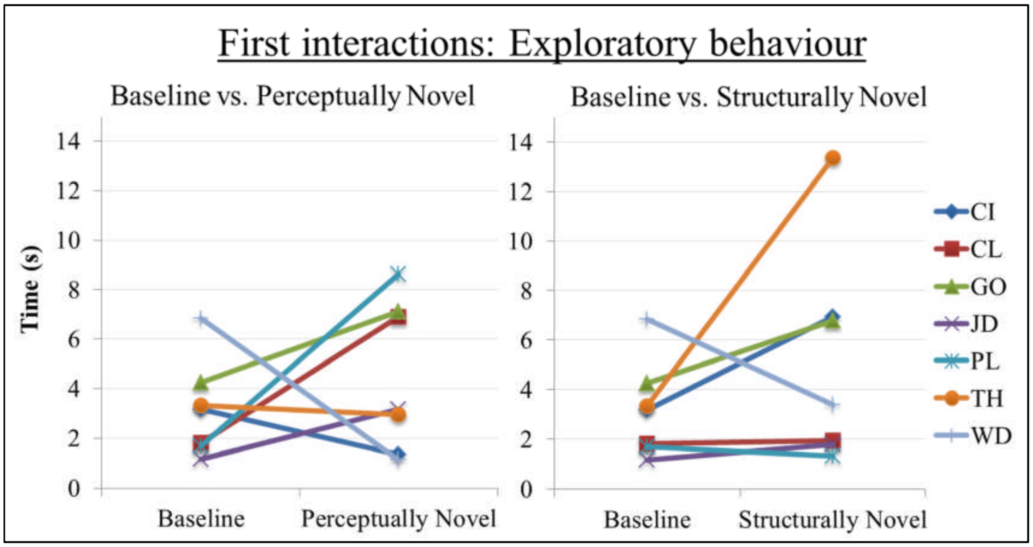


Figure 8. Total amount of time birds spent exploring baseline versus perceptually novel, or baseline versus structurally novel objects during first 15 seconds after experiencing the object's structural properties.

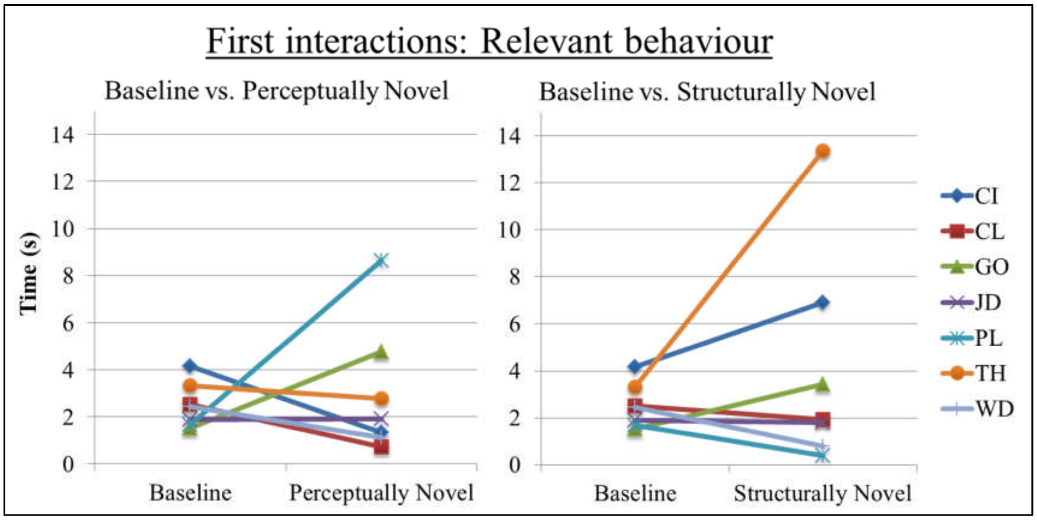


Figure 9. Total amount of time birds spent performing relevant behaviours on baseline versus perceptually novel, or baseline versus structurally novel objects during first 15 seconds after experiencing the object's structural properties.

It could be predicted that biases for specific colours might influence whether birds came into the target zone for specific objects. When grouping objects from both sets by colour, a Friedman test revealed no significant difference in the proportion of time spent in the target zone for differently coloured objects (χ^2_2 = 0.00, N = 7, p = 1.00),

Finally, a Fisher's exact test was used to determine whether tool-using individuals were more likely to interact with novel objects in their aviary. While all tool-using birds (5/5) interacted with the objects, they were not significantly more likely to interact with objects relative to non-tool-using birds (2/5; p = 0.167).

Study 2 discussion

Study 2 provides preliminary evidence that vasa parrots attend to the structural properties of the objects they interact with. This is evidenced by an increase in the amount of time they spend performing relevant behaviours on structurally novel objects relative to baseline objects, suggesting that individuals are attempting to gain some information about the physical affordances of these novel objects.

By presenting three visually distinct (differently coloured) objects, this paradigm allowed for discrimination of whether the birds' haptic exploration is driven by perceptual novelty alone, or primarily by a change in the object's underlying structure. The results showed that there was no significant difference in birds' duration or quality of exploration when exploring perceptually novel objects relative to baseline objects, suggesting that in this species, exploration is not driven by visual novelty alone. This result is consistent with developmental studies of infants which, from six months of age, do not increase their exploration of objects that are novel in colour only, but do increase their exploration when the object is visually identical, but varies in a haptic property such as temperature (Bushnell *et al.* 1985).

Demery (2013) found that kakarikis show a significant increase in exploration when presented with either visually or structurally novel objects relative to a baseline object, but that this difference was greatest for structurally novel objects, and least for objects that had changed only in colour. Furthermore, the kakarikis showed a significant increase in the diversity of exploratory behaviours directed toward structurally novel objects, which was surpassed only by the diversity of exploration toward changes in shape. Although the vasas did not appear to increase their exploration of visually novel objects relative to baseline objects, they did show a significant change in the quality of exploration directed toward structurally novel objects, similar to the kakarikis.

The vasas' differential behavioural response toward structurally novel objects is also consistent with developmental studies, which show that after becoming habituated to certain object types in the absence of visual feedback, infants spend a greater amount of time holding objects that differ in shape, weight or rigidity (Streri & Spelke 1988; Streri *et al.* 2000). In particular, the change in the quality of the birds' exploration toward structurally novel objects is in line with research showing that infants also gear their exploration toward the novel property of the objects they encounter, for example by stroking objects that have changed in texture, or rotating objects that have changed in shape (Ruff *et al.* 1984).

Although the aims of this study were different, these results contrast with Povinelli & Dunphy-Lelii's (2001) data suggesting that although chimpanzees may change their behaviour to explore small visual differences in objects, they do not change their behaviour to explore visually familiar objects that violate their previously formed expectations of how that object should behave. These differences may also be attributed to the different aims between studies – in Povinelli and Dunphy-Lelii's study, where the subjects were trained to manipulate the objects in specific ways in order to achieve a goal (a food reward). With this goal in mind, the chimpanzees may not have been attending to the structure of the stimuli but simply repeating the action for which they were typically rewarded, whereas the children seemed to take time to explore potential causes for this difference in behaviour.

In contrast to the children in Povinelli and Dunphy-Lelii's study, the vasas did not show any immediate increase in functional behaviour after their expectations about the behaviour of the object had been violated; that is, after first experiencing the structural properties of the object (for example, by picking up a rigid piece of rope), there was no immediate increase in functional behaviour during the first 15 seconds of encountering structurally novel objects relative to baseline objects. Instead, the vasa's exploration appears to change on a more gradual level. Unfortunately, few other studies appear to include this more fine-grained analysis of the immediate reactions to novelty, and as a result it is difficult to compare these data with other species, including human infants.

Steele and Pederson (1977) were among the first to note that, after familiarization to an object, changes in exploratory behaviour should be predicted to occur primarily within the modality in which the novelty of the object is most salient; in their experiments, for example, they found that dishabituation of looking time, but not manipulation time, was produced when infants were presented with visually novel (differently coloured) objects, but that manipulation time was only increased for structurally novel objects. This would have been interesting to examine in the vasas but was not possible due to a number of reasons; namely that looking times would have been exceptionally difficult to code due to the birds' laterally located eyes and that the objects were presented in the home aviary where all birds had visual access to them at all times.

The data from this study show that vasa parrots have a broad repertoire of exploratory behaviours, using the tongue, beak and foot to manipulate objects. Following Steele and Pederson's (1977) idea of tailored exploration, it could be predicted that exploration of structural object properties should be further tuned to the novel property *within* that modality. Given the vasas' diverse exploration, an interesting avenue for future research would be to examine whether the finer, more specific manipulations of the birds are geared toward the property of interest, for example by changing texture versus weight. Unfortunately this was not possible to examine in this study as both object sets used required similar behaviours in order to gain information about their properties.

One limitation to this study is that the data reported are from a small number of individuals (N = 7) and only two object sets. Unfortunately, due to limitations at the research site it was not possible to collect additional data using additional object sets, however further data from a larger number of birds and using additional objects would create a more reliable picture of how these birds attend to various physical properties. Additionally, as the objects were presented in a group context, it was not possible to ensure the same individual level of habituation to each object as the infant studies do. Given that the data still showed a difference in exploration quality, including this in future paradigms may reveal a more pronounced difference. Notably, neither of the two wild-caught birds (UF and BW) was included in the analyses as they did not approach or interact with the objects. This may have been due to their background, as previous studies have shown reduced neophobia and greater exploratory tendency in captive-bred animals (Yoerg & Shier 1997; McPhee 2003a; Benson-Amram *et al.* 2013). As these two birds are also believed to be the oldest in the group, it is difficult to determine whether their lack of interest in the objects was due to their age or background.

This study has a number of strengths; specifically, this paradigm capitalizes on the vasas' natural propensity to explore objects and, as highlighted in the this study's introduction, features low cognitive demands as it occurs outside of a problem-solving context, and requires no pre-training. Crucially, this task is also easily adapted to a range of species and can be used to collect useful comparative data on how species from different environments and taxa perceive and attend to objects in their environment.

General discussion

The observational data on tool use among greater vasa parrots provides not only the first evidence of tool use in these birds, but also data on a novel form of tool use that had previously only been documented among humans. Furthermore, the experimental data suggest that these birds attend to hidden object unobservable properties, which may translate to more creative or flexible tool use in contrast to innate, hardwired tool-using behaviour (Tebbich & Bshary 2004).

Taken together, these data are in line with the idea that exploratory animals are more likely to innovate novel foraging strategies such as tool use, either as a result of the information gained from their exploration or the increased probability of performing novel behaviours which may translate to functional tool use. In line with this proposed relationship between tool use and object manipulation, all 5 tool-using birds interacted with the objects in Study 2, compared with only 2/5 non tool-using birds. Unfortunately, however, the sample size was too small for a significant difference to be found.

The link between exploration and problem solving could be further explored in order to answer several questions that are raised from this study. Although these birds appear to be changing their exploration in order to gain information about the structural properties of objects they interact with, it is unclear whether vasa parrots (or parrots in general) are actually capable of remembering and then applying this information in a causally relevant context to solve problems. Additionally, although most parrot species including the vasa are highly explorative, to date there has been no research examining what actually drives this exploration. Are the animals actively attempting to gain functional information about the objects, or is the change in their behaviour more simply a response to novelty? These questions are addressed in Chapter 5.

Based on these observations and experimental results, the vasa parrot represents a new species of interest for future studies of physical cognition. As an overwhelming amount of research investigating physical cognition is focused on chimpanzees and corvids, parrots can be viewed as a welcome addition which will allow for further comparisons between species and ultimately allow us to better assess the evolution of complex cognitive abilities in a range of species, including humans.

Chapter 5. Function and Flexibility of Object Exploration in Kea and New Caledonian Crows

Abstract

As discussed in Chapters 2 and 4, a range of nonhuman animals frequently manipulate and explore objects in their environment, which may enable them to learn about physical properties and potentially form more abstract concepts of properties such as weight and rigidity. However, whether animals can apply the information learned during their exploration to solve novel problems, and whether they change their exploratory behaviour to seek functional[1] information about objects has not been fully explored. I presented kea and New Caledonian crows with sets of novel objects to explore both before and after encountering a task in which the objects could function as tools. Following this, subjects were given test trials in which they could choose from among the objects they had explored to solve a tool-use task. Several individuals from both species performed above chance on these test trials, and only did so after exploring the objects, compared to a control experiment with no prior exploration phase (although one subject performed significantly above chance in this control experiment). These results suggest that selection of functional objects as tools may be guided by information acquired during exploration. Neither kea nor crows changed the duration or quality of their exploration after learning that the objects had a functional relevance, suggesting that birds do not adjust their behaviour to explicitly seek this information.

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[1] Note that most of an object's structural properties are necessarily functional as they predict how that object behaves within its environment and in relation to an organism, however as this chapter focuses extensively on tool use and problem solving, the term functional will be used throughout to refer specifically to those properties which allow the object to be used to solve a specific physical problem.

Introduction

The empirical data presented in Chapter 4 contribute to a growing body of evidence that unrewarded object exploration provides individuals with information which may aid in forming predictions about their physical environment, and that individuals may structure their exploratory behaviour in order to refine these predictions once they are violated (Chappell *et al.* 2012; Bateson & Martin 2013; Demery 2013, appendix F). Exploration may therefore allow individuals to develop more abstract concepts about ‘invisible’ physical properties such as weight and rigidity, which could provide a route to flexible problem solving and tool use. The exploratory play of young humans is thought to scaffold such learning (Piaget 1952). Consequently, unrewarded object exploration may serve as an important phylogenetic or ontogenetic precursor to tool use, although whether any animals can use information gained from exploration to solve problems is little studied, and we do not know if any nonhuman animals can use exploration strategically to gain such information.

Some of most pronounced object exploration is found among large-brained birds and primates, with tool-using species generally exhibiting higher rates of object exploration than non-tool-using species (Glickman & Sroges 1966; Parker 1974; Torigoe 1985; Auersperg *et al.* 2015). For example, early comparative studies of 74 primate species found that tool-using *Cebus* (Torigoe 1985) and great ape species (Parker 1974; Torigoe 1985) show a broader repertoire of manipulations than non-tool-using primate species, or spend more time manipulating detached objects during development than closely related species which do not habitually use tools (chimpanzees versus bonobos: Koops *et al.* 2015). Among birds, some species of corvid and parrot readily explore and play with objects, with these same species demonstrating sophisticated problem-solving abilities in captivity as well as spontaneous and habitual tool use (e.g., Goffin cockatoos and New Caledonian crows; Hunt 1996; Auersperg *et al.* 2012; Auersperg *et al.* 2015). Recent comparative studies within parrots and corvids have additionally shown that species proficient in tool use either in the wild or in experimental contexts showed high frequencies of combined object manipulation compared to non-tool-using species, either during ontogeny or in adulthood (Kenward *et al.* 2011; Auersperg *et al.* 2014a).

Despite this evidence, the nature of the link between object exploration and tool use is relatively unexplored. What drives exploratory behaviour and what (if any) information is being gained from exploration of an object that may later translate to its functional use? An early study of chimpanzees provides some evidence that individuals acquire information about the functional properties of objects after manipulating them in a play context. When presenting six captive chimpanzees with a stick to rake in a food reward, Birch (1945) found that only two subjects (one of whom had previous experience playing with sticks) successfully solved the task within 30 minutes. All subjects were then presented with sticks in their enclosure over the course of three days, during which time they played with the sticks extensively and began using them as a functional extension of the arm. When presented with the task again, performance was markedly different, with each animal immediately picking up the stick and solving the problem within 20 seconds. This suggests subjects learned something about the functionality of the sticks from their exploration, however as the same sticks were used in the test trials it is unclear whether performance was reliant on the chimps' familiarity with the materials, or whether it reflected an abstract understanding of the tool's functional properties (i.e., rigidity) that had been formed during repeated interaction with the objects (Manrique *et al.* 2010).

A few studies have more explicitly addressed the role of experience in learning about an object's functionality. Manrique et al. (2010; 2011) presented individuals from three great ape species and capuchins with a task in which they were required to select a rigid tool from a set of three novel, but visually distinct objects after i) manipulating the objects themselves, ii) watching an experimenter manipulate the objects and iii) a control condition with no demonstration or manipulation. Great apes performed significantly above chance in all three conditions, but great apes and capuchins performed significantly better when manipulating the objects themselves or after watching a demonstration by the experimenter than in the control condition. These results suggest that great ape subjects were able to use visual static information alone to select the objects, although performance for all species was enhanced by experience with the objects' properties.

In contrast, Povinelli and colleagues found that chimpanzees performed at chance levels on tasks distinguishing between identical heavy and light, or near-identical rigid and pliable objects as tools, despite demonstrations of the objects' properties by an experimenter and multiple exposure sessions in which they could interact with the objects immediately prior to test trials (Povinelli 2000, p163-170; Povinelli & Ballew, p162-170; but see Furlong *et al.* 2008). The authors conclude from this and other, related experiments that while chimpanzees are proficient at using perceptual stimuli to solve problems, they do not form abstract concepts of hidden properties or unobservable phenomena (Povinelli 2000, p300). However, one key difference between these studies is *when* the animals were allowed to explore the objects. For example, the subjects in Manrique *et al.* (2010; 2011) and Furlong *et al.* (2008) were allowed to briefly explore the objects after first being trained on the tool-using task, and did so in the testing compartment in view of the (non-baited) task. Therefore in contrast to the subjects in Povinelli (2000) which explored the objects prior to experience with the task, these subjects had information about the functional relevance of the objects as they encountered them, which may have influenced which particular properties of the objects they attended to.

There is therefore some evidence that chimpanzees and capuchin monkeys can learn about objects through exploration (Manrique *et al.* 2010; Manrique *et al.* 2011), though the degree to which this involves abstract representations of object properties such as weight and rigidity remains a matter for debate (Povinelli & Penn 2011; Seed *et al.* 2011). A related question concerns whether or not exploration can be used strategically to seek information. Individuals might incidentally gain information about the objects' hidden, structural properties as they are manipulated, but does exploration differ depending on whether it is driven by information seeking (e.g., manipulating a branch in passing after eating, or manipulating a branch with the goal of selecting a probing tool)? That is, do individuals alter the quality or duration of their exploration to learn about these properties once they have a task in mind? This type of behaviour is evident in young children who increase their exploration in order to learn about causally ambiguous stimuli (Schulz & Bonawitz 2007). Similarly, when choosing among stone tools for nut-cracking, wild capuchin monkeys resort to techniques such as tapping or moving stones that do not possess reliable visual cues about weight as a functional property (e.g., when choosing between identical stones, or when larger stones are lighter than smaller stones; Visalberghi *et al.* 2009). In contrast, chimpanzees do not change their exploratory behaviour in order to seek explanations about why familiar objects suddenly function differently in the absence of visual cues (Povinelli & Dunphy-Lelii 2001).

Most research aimed at investigating whether other species represent functional features have focused on primates, and typically on tool-using species due to the assumption that tool use reflects enhanced physical cognitive abilities (e.g., Povinelli 2000; Furlong *et al.* 2008; Schrauf *et al.* 2008; Manrique *et al.* 2010; Manrique *et al.* 2011; Povinelli & Ballew 2012; Schrauf *et al.* 2012; Sabbatini *et al.* 2014; but see Santos *et al.* 2006). Further research on both tool-using and non-tool-using species outside of the primate order is needed to determine whether i) information about object properties is gained through exploration and can be applied in a problem-solving context; and ii) what drives exploratory behaviour.

I presented kea, a highly explorative species that can use tools in captivity but does not use tools in the wild, and New Caledonian crows, proficient tool users and manufacturers in both wild and captive settings, with a series of experiments to investigate the function and flexibility of exploration in learning about structural object properties. In Experiment 1, birds were presented with sets of novel objects to explore, which were similar in size, shape and material, yet varied in terms of their underlying structure (e.g., 10 identically sized wooden blocks, half of which were heavy and half of which were light). Each of these objects possessed a unique colour/pattern combination and was therefore visually distinct, but one of these features served as reliable indicator of the object's underlying structure while the other did not (e.g., all heavy blocks had striped patterns and all light blocks had dots, while colour was irrelevant). Subjects were allowed to explore these objects in two phases, both before (Phase 1) and after (Phase 3) encountering a task in which a similar object could be used as a tool (e.g., a heavy black block; Phase 2). Following this, I tested whether subjects gained relevant information from their exploration by presenting them with test trials (Phase 4) in which subjects could choose between two objects (one functional and one non-functional) they had previously encountered in Phases 1 and 3 in order to solve a task. In Experiment 2, I investigated whether subjects could more easily generalize information about structure when this was associated with colour by presenting subjects with an additional set of heavy and light blocks, this time with colour rather than pattern as the relevant feature. Finally, subjects' performance in Experiments 1 and 2 was compared to test trials featuring a new set of objects that subjects did not have the opportunity to explore or interact with prior to testing (Experiment 3).

If exploration provided information about structural object properties, it was predicted that subjects would perform significantly better in Experiments 1 or 2 in which they were allowed to explore the objects prior to testing, than in Experiment 3 when they were not allowed to explore. It was expected that birds which spent longer exploring objects or spent more time engaging in functional behaviours (defined here as behaviours that are likely to reveal the hidden structural properties of the object, such as picking up a heavy block, in contrast to touching it with the beak without moving it) during exploration phases would perform better in the test trials. If the information gained during exploration was specific to each unique object explored, rather than a more general understanding of the contingency between structure and visual features (e.g., pattern), it was predicted that subjects would be more likely to choose correctly on trials featuring objects they had previously chosen to explore and had direct contact with (Experiment 1). If subjects' exploration was driven by information seeking, they were expected to either increase the amount of time they spent exploring or to qualitatively alter their exploratory behaviour after the tool use training (Phase 3) in which they had experience that the properties of the objects were functionally relevant, compared to pre-tool use training (Phase 1, Experiment 1). Alternatively, if exploration was driven by visual novelty, a significant decrease in exploration from Phase 1 to Phase 3 was expected.

General methods

Subjects

Kea

Subjects were 8 captive-born, adult kea (7 males and 1 female) housed at the Haidlhof Research Station (University of Veterinary Medicine and University of Vienna) in Bad Vöslau, Austria. All subjects were housed together in a group aviary (approximately 520m^2). Testing took place in mornings (8am to 10am) and afternoons (1pm to 4pm) roughly 30 minutes after feedings. For all training and testing sessions, the birds were rewarded with 1/8 a piece of peanut (a preferred food). The birds had previously participated in numerous cognitive experiments, including multiple tool use studies where birds learned to insert stick tools, small blocks and balls into the opening of either a Perspex box or a Perspex tube in order to obtain a reward (e.g., Auersperg *et al.* 2010; Auersperg *et al.* 2011; Gajdon *et al.* 2011). Additionally, the kea had previously participated in a study focusing on object exploration, where subjects were presented with sets of novel objects including wooden balls, blocks, rings and sticks to explore freely (Auersperg *et al.* 2014a), Unlike the present study, subjects were not required to use these objects as tools after exploration. Although these previous experiments meant that the birds had experience with tool use tasks and may therefore have already learned about the functional properties of these tools (e.g., the birds had a good amount of experience using a rigid object as a stick tool), this is not predicted to affect the current experiment, which focuses primarily on within-subject differences in exploration and whether birds can use information from exploration to choose functional objects. To my knowledge, the birds had never had experience with a setup that tested their knowledge gained after exploring objects, or requiring them to choose between functional or non-functional objects based on structural properties.

Crows

Subjects were 6 wild-caught New Caledonian crows (2 juvenile males; 2 adult males and 2 adult females) housed in captivity at the Department of Psychology, University of Auckland research site in Farino, New Caledonia for approximately 5 weeks prior to the start of testing. Age was determined from mouth colouration and sex was determined from body size. The birds were separated in small groups of up to 3 individuals (usually as family groups) and housed in separate aviaries measuring roughly $2m^2$ x 3m. For all training and testing sessions the birds were rewarded with a small piece of meat (roughly 3mm x 3mm). The birds were tested in the mornings (8am to 12pm) and afternoons (2pm to 5pm) roughly one hour after regularly scheduled feeding times. Prior to testing, all birds had been trained to drop stones into a Perspex box, causing a platform to fall and release a reward. During testing the birds concurrently participated in a hand tracking study (Jelbert *et al.* 2016), but otherwise had no experience with tasks that required them to attend to structural object properties.

Experiment 1: Learning about weight and rigidity through exploration

Experiment 1 was aimed at determining whether exploration provided birds with information about the structural properties of objects that would enable them to subsequently choose a functional tool in a tool-use task, and whether subjects changed the quality or duration of their exploration to learn about these properties after they had experience that some of the objects could function as tools. All test phases are outlined in Table 8 for clarity and are described in further detail under Procedure.

Table 8. Overview of test phases, shown in order of occurrence, in Experiment 1.

Phase	Description
Phase 1	Object exploration sessions (pre-training)
Phase 2	Subjects trained on tool-use task
Phase 3	Object exploration sessions (post-training)
Phase 4	Test trials

Setup and apparatus

Both species were tested with two different object sets, each of which focused on a distinct structural property (ropes: rigidity; blocks: weight). Each set consisted of 20 categorically similar objects (e.g., 20 lengths of rope, all identical in size and material) that varied in terms of their observable (colour, pattern) and unobservable properties (structure – in the case of the ropes, half had a stiff piece of wire in the middle). For each object set, one of the observable features (e.g., colour) corresponded with the structure of the object, while the alternative feature was irrelevant (e.g., pattern). These two opposing features were included to make it more difficult for the birds to learn over the course of the test trials which objects were functional if they had not learned these contingencies during exploration. It also ensured that the objects used on each trial were visually unique so that birds would not continue to choose the same object they were rewarded for on previous trials, a potential confound in other studies (discussed in Manrique *et al* 2010). Half of the subjects were first tested with the block set, while the other half were first tested with the rope set.

Blocks/weight

The ‘weight’ object set consisted of 20 wooden blocks (4 x 4 x 4cm), half of which were light (45 grams) while the other half were heavy (125 grams). The relevant observable property for weight was pattern, such that all heavy blocks featured a striped pattern and all light blocks featured dots (Figure 10a). Ten different colours were used within the set, with each colour featured on both a heavy and light block, thus making it an irrelevant feature. Due to size restrictions, the crows were presented with an analogous set of objects consisting of small clay balls (2cm diameter), with the heavy balls weighing 0.44 grams and the light balls weighing 0.04 grams.

For the test trials (Phase 4, described below), the birds had to drop the blocks or balls into an opening in the top of a Perspex box (Figure 10a; Bird & Emery 2009). If the birds correctly selected a heavy, functional block, the weight of the block would cause a platform within the box to collapse, consequently releasing a reward from an opening in the bottom of the box. In order to prevent mistrials, the platform was held in place by an electromagnet that was operated remotely by the experimenter, so that when subjects inserted the correct object, the experimenter pressed a button on a remote that was hidden behind a clipboard held by the experimenter throughout the session, causing the platform to collapse.

Ropes/rigidity

The ‘rigidity’ object set consisted of 20 pieces of rope (13cm long, 0.75 cm diameter), half of which had a piece of gardening wire inserted in the middle, thus allowing the rope to function as a stick tool, and the other half of which were flexible and non-functional (Figure 10b). The relevant observable property for the ropes was colour, so that all of the functional ropes were blue, for example, while the other half were yellow. Pattern was an irrelevant feature, with one functional and non-functional object marked with identical patterns so that the object set featured 10 different patterns in total.

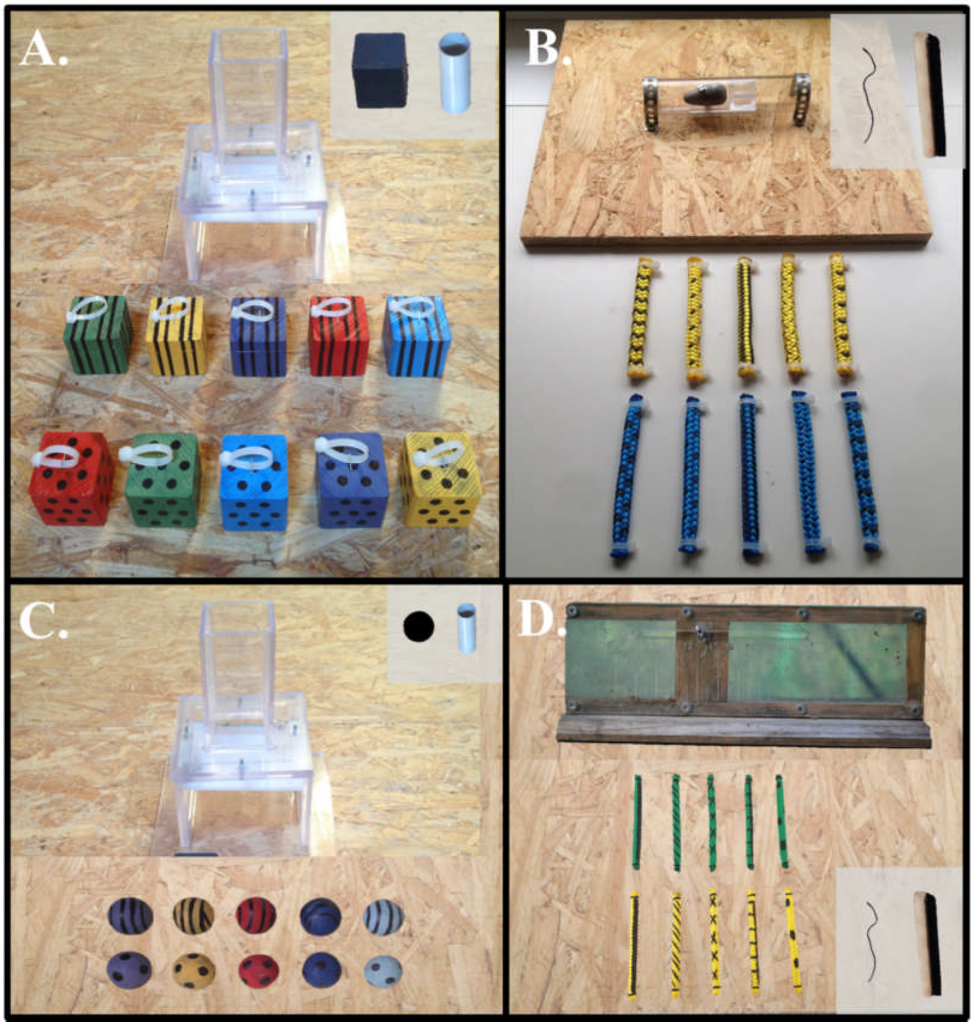

Figure 10. Example object sets and apparatuses used with the kea (A, B) and crows (C, D). A, C) Block set: individuals must select a heavy block or ball (weight corresponds with pattern; heavy blocks are striped) to insert into the opening of the box to collapse the platform inside. B, D) Rope set: subjects must choose a rigid rope (rigidity corresponds with colour) to retrieve the food.

For the test trials, subjects had to select a functional rope with a wire inserted in order to push a reward out of a Perspex tube (3.5cm diameter, 11cm long) mounted to a wooden board (Figure 10b). The reward was presented in a small Perspex box attached to a weight (115 grams) to ensure that it could only be dislodged with the functional rope. Due to species differences, a separate apparatus was used with the crows so that subjects raked in, rather than pushed, their food from an artificial crevice (opening 1.5cm x 11cm). For both apparatuses the reward was always presented at the same distance from the opening across trials.

Testing compartments

Kea

For the kea, all object exploration trials (Phases 1 and 3 described below) took place in the waiting compartment, while test trials (Phase 4) took place in the neighbouring testing compartment. The waiting and testing compartments were attached to the main aviary and featured opaque sliding doors so that subjects were in visual, but not auditory isolation from conspecifics. The experimenter was visible throughout exploration and test trials, and during test trials, was present in the same compartment as the subject but remained motionless with gaze fixed on the apparatus until the subject made a choice, at which point the experimenter removed the remaining object. The experimenter stood next to the entrance to the testing compartment, so that subjects walked into the compartment and immediately had their backs facing the experimenter as they selected an object.

Crows

Both exploration and test trials took place in a designated testing aviary attached to each group's main aviary, such that each group had its own distinct testing compartment. As the crows were wild-caught and less habituated to human presence, the experimenter was never visible and remained on the outside of the testing compartment filming all interactions during object exploration trials. This ensured that the birds felt fully comfortable coming down to explore the objects. This difference in procedure is not expected to influence the results, as the kea rarely attended to the observer presence during exploration trials. Throughout test trials, the experimenter only entered to re-bait the apparatus and begin a new trial.

Procedure

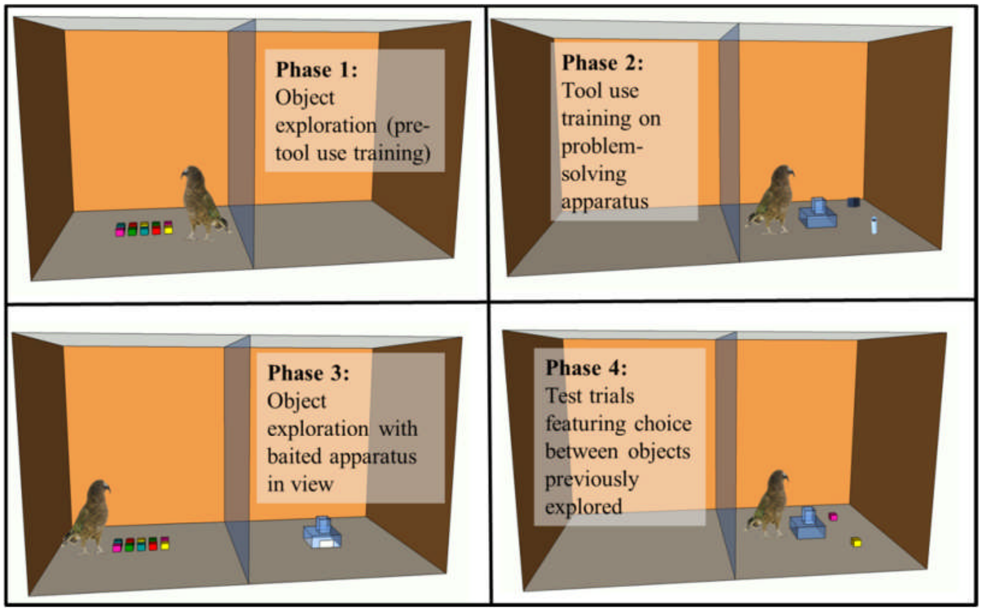

Figure 11. Overview of experimental phases, showing two compartment setup, and which items are presented to subjects during the different phases. Note that with the exception of the habituation phase (1b, described below), experimenter visibility (not visible for the crows) and the use of only one compartment, rather than two, for the crows, the procedure for both species was identical.

Phase 1. Object exploration (pre-training)

This stage served as a baseline measure of how subjects interacted with the objects prior to encountering a task in which they could be used as tools. Ten of the twenty objects (five functional, five non-functional) were presented in the compartment, either on the floor (kea; see Figure 11a) or a table (crows). Subjects were given ten minutes to explore the objects, during which time the experimenter filmed all interactions and commentated which objects were being explored. If subjects did not interact with any of the objects during the first ten minutes of the first session (as was the case for most of the crows), this procedure was paused and they were presented with several additional steps in order to first overcome potential neophobic responses while ensuring subjects did not over-habituate to the objects such that they would become an irrelevant feature of the birds' environment (described below). Trials lasted up to thirty minutes, or until ten minutes after subjects first made physical contact with the objects. Subjects moved on to Phase 2 after they explored at least three exemplars of a functional and non-functional object (6 total), or after a maximum of four sessions.

Phase 1b. Habituation

For individuals that failed to interact with the objects during the first 10 minutes of encountering them, a habituation phase was introduced. This was needed for most of the crow subjects. During these habituation sessions the objects were once more placed in the testing compartment but were now placed next to 10 small pieces of meat so that subjects had walk past and remain near the objects in order to retrieve all of the pieces. These individual habituation trials lasted 30 minutes for each bird. If subjects i) consumed all of the meat within one standard deviation of the time it took in baseline trials with only meat present and no objects (collected prior to the start of the experiment) and ii) didn't show any startle behaviour (e.g., jumping jacks) when approaching the objects, they began their first post-neophobia exploration session the following session. If subjects interacted with any of the objects by picking them up in the beak, a ten minute timer was started from the moment of contact, and these ten minutes were considered the subject's first post-neophobia exploration session.

If subjects still did not meet the criterion for retrieving the meat after three sessions, the objects were then presented in the subjects' home aviary with meat nearby for up to three hours over two days, where all birds within that family group could see and potentially interact with the objects. If the target individual interacted with the objects during this time this was counted toward their criterion for number of objects explored, and individual exploration sessions began the following day. If subjects still did not interact with objects during this time they were given a maximum of four more individual habituation sessions before being excluded from the study. No birds were excluded due to neophobia.

Phase 2. Tool use training

Weight. After their initial exploration sessions, subjects were then trained on a tool-using task in which they were required to choose between a functional, heavy object (a heavy solid-black block weighing 125g, or ball weighing 0.44g for the crows) over a non-functional, light object (a hollow, plastic grey pipe: 4cm long, 2.5cm diameter, weight: 0.004 grams) to drop into the opening of the box to collapse the platform inside and retrieve a reward. Subjects were trained in a step-wise manner, so that initially, the block (or ball) was resting on the edge of the opening so that it could be nudged in. After the birds nudged in the block on three consecutive trials, it was then placed on the surface in front of the apparatus so that subjects were required to pick it up and place it in the opening.

After three consecutive successes, the birds then moved to the final stage of training in which the tool and a non-functional object were presented equidistant from either side of apparatus (side of correct object counterbalanced across trials) and subjects were required to select the correct object and carry it to the apparatus for use (Figure 11b). Once subjects made physical contact with one of the two objects, the experimenter approached from the other side and removed the remaining object. As the crows were less habituated to close human presence, the experimenter remained hidden outside of the testing compartment. If the bird attempted to approach the second object, the experimenter gave a soft knock on the door of the compartment, causing the crow to leave the testing table while the experimenter entered to remove the second object, after which the bird would come back down to the table to complete the task. Subjects completed tool use training after choosing the heavy black block on five consecutive trials.

Rigidity. Subjects were required to choose between a functional, wooden stick tool (13cm long, 1cm diameter) over a non-functional piece of string (22cm long, 0.5cm wide) to retrieve a reward from a clear, Perspex tube (kea) or artificial crevice (crows). Notably, the non-functional training item was most similar in material to the objects presented during exploration, whereas the opposite relationship existed for the weight set (the functional training item was a block). This difference is not predicted to influence the birds' preferences for particular objects in exploration or test trials unless they are relying on structural information. This is because these trials all featured objects that were similar in appearance, such that subjects could not easily develop a preference for one object type over another based on visual similarities to the training objects.

Subjects were again trained in a step-wise procedure using the same criterion for progress as the weight set, beginning with the stick tool already inserted into the tube or crevice. This task proved difficult for some kea (AN, LI), who were unable to retrieve the reward after several sessions with the stick tool inserted in the tube. These subjects were instead trained using the Perspex box apparatus from the block set, but with a new Perspex tube (height: 5cm, diameter: 5cm) on the top as the opening. Subjects were required to insert one end of the stick tool into the tube so that it made contact with the platform, and then apply enough force on the distal end of the stick to collapse the platform. These subjects were subsequently tested in Phase 4 using the same box apparatus.

Phase 3. Object exploration (post-training)

This stage allowed me to measure any differences in exploration patterns after subjects had encountered a task in which objects similar to those they explored could be used as tools. After meeting training criterion, birds were presented with the remaining ten objects (half functional, half non-functional), and were again given 10 minutes for exploration upon first contacting an object (Figure 11c). Different objects from those presented in Phase 1 were used (e.g., new colours or patterns) to reduce the likelihood that subjects would lose interest in the objects. In this stage, the apparatus used during training was baited and presented in full view while the subjects explored the objects to ensure that they could have the task in mind. For the kea, birds needed to walk past the apparatus in the testing compartment to enter the waiting compartment, and once in the waiting compartment the apparatus remained fully visible. For the crows, the apparatus was presented in the same compartment, but featured Perspex coverings to each of the openings so that birds could not use the objects on the apparatus in any way. The number of sessions subjects were given in this phase matched the number of sessions they were given in the first phase, such that if subjects had two exploration sessions in Phase 1, they were given two exploration sessions in Phase 3.

Phase 4. Test trials

To test whether birds had encoded information about the properties of the objects they explored, subjects were presented with one test session of 10 trials in which they could choose between a non-functional and a functional object from the set of objects they had previously encountered. The setup was identical to that used in Phase 2, where the objects were presented equidistant from either side of the apparatus (Figure 11d), with the side of the functional object pseudorandomized and counterbalanced across trials. The objects were paired randomly such that half of the trials featured objects from the same exploratory phase, whereas the other half featured one object from Phase 1 and one object from Phase 3. Between trials the experimenter re-baited the apparatus and placed new objects, all out of sight of subjects. If subjects did not make a choice within three minutes, or chose an object but did not carry it to the apparatus to retrieve the reward, a new trial was started and the incomplete trial was repeated at the end of the session.

Behavioural data

All object exploration sessions (Phases 1 and 3) were coded in the Observer XT Version 10. A random selection of 11 videos (17%) was independently re-coded by a research assistant uninvolved in the study and blind to whether the session was pre- or post-tool use training, as well as which objects were functional versus non-functional. Interobserver reliability was substantial (Cohen’s kappa = 0.70) indicating the videos had been coded reliably.

Each interaction with the objects (when subjects were in physical contact with an object) was coded as a single bout, and each bout was coded hierarchically by assigning it to the behaviour category of whichever behaviour within the bout provided the most information about the structural properties of the object. For example, if a subject moved an object on the substrate before picking it up in the beak, this entire bout was coded as ‘pick up with beak’, whereas if the subject had only contacted the object with the beak, the bout was coded as ‘contact with beak’ (see Table 9 for ethogram). Behaviours that likely provided information about the structural properties of the objects, such as picking up with a heavy block, were further classified as ‘relevant’ behaviours (specified in Table 9).

These behavioural data were then converted into several proportional measures for subsequent analyses. Both general exploratory behaviour (all behaviours in Table 9, including relevant behaviours) and relevant behaviours were examined as a proportion of the total trial time, either overall or separately for pre- and post-training sessions (Phase 1 and 3). Exploration of functional versus non-functional objects was measured as a proportion of the time the individual spent exploring the objects.

Table 9. Ethogram of behaviours coded for object exploration sessions, including which behaviours provided information about the structure of the different object sets (i.e., relevant behaviours). Behaviours are listed in their hierarchical order.

Behaviour	**Description**	**Relevant?**
Throw	Object is picked up from the substrate and momentum is used when releasing it from the beak, so that it travels some distance in the air rather than dropping straight from the beak.	Ropes, blocks
Drag-throw	The subject begins by dragging the object across the substrate with the beak, and the object breaks contact with the substrate while being dragged.	Ropes, blocks
Pick up with beak	Bird picks up the object with the beak so that it is no longer in contact with the surface it rests on (blocks) or only one end is in contact with surface (ropes) but does not throw or bring object into contact with any other surfaces or free objects.	Ropes, blocks
Pick up with foot	Bird picks up the object with the foot so that it is no longer in contact with the surface it rests on (blocks) or only one end is in contact with surface (ropes).	Ropes, blocks
Insert	Bird inserts the object through the fence or into a nook or crevice and completely lets go with the beak.	Ropes, blocks
Probe	Bird inserts the object through the fence or into a nook or crevice and retracts it entirely.	Ropes, blocks
Drag	Bird drags the object across the ground without the object leaving the substrate.	Ropes, blocks
Move with beak	Bird pushes object on substrate while contacting but not holding with the beak. Moves are classified as greater or less than 5cm[2]. Moving was not considered a relevant behaviour for the ropes as these had a thicker material such that they usually retained their straight shape when moved.	Blocks (>5cm)
Move with tool	Bird uses a stick tool to move the object while maintaining contact between the tool and object for the duration of the behaviour.	Blocks (>5cm)
Move with foot	Bird pushes object on substrate while contacting with the foot.	Blocks (>5cm)
Turn	Specific to the block set: Kea turns the block over with the beak or foot so that it is now resting on a new side.	
Contact with	Bird contacts the object with both the beak and foot	

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[2] This criterion was selected in order to provide a conservative estimate of whether the individual experienced the weight of the block by moving it more than its entire length.

beak and foot	without moving the object on the substrate.	
Contact with beak	Bird contacts the object with the beak (e.g., biting, touching with the outer part of the beak, etc.) without picking up the object or moving it on the substrate.	
Contact with foot	Bird contacts the object with the foot but does not pick up or move on substrate.	

Analyses

All data were analysed in IMB SPSS Statistics version 21, using two-tailed tests with the significance level set at $p < 0.05$. Exact p-values are reported for all tests (Mundry & Fischer 1998). Data are reported from seven kea (blocks: N = 7; ropes: N = 6) and six crows (blocks and ropes: N = 6). Eleven individuals participated in experiments for both object sets (six crows and five kea) and two kea participated in the experiment for only one object set.

Do birds learn from their exploration?

To determine whether, as a group, subjects performed above chance on test trials following exploration, a one-sample Wilcoxon signed-rank test was used. To determine whether performance on the test trials was predicted by individuals' duration or quality of exploration across all exploration sessions (Phases 1 and 3 grouped), and whether this differed between species, a binomial GLMM (GLMM1) with a logit link function was run with proportion of correct trials as the target variable. Fixed factors entered into the model were i) total proportion of trial time spent exploring the objects (pre- and post-exploration grouped), ii) total proportion of trial time spent engaging in relevant behaviours (pre- and post-exploration grouped), and iii) species. Each individual had one data point per set entered into the model (N = 7 kea and 6 crows for the block set, N = 6 kea and 6 crows for the rope set), resulting in 25 data points. Subject and object set were entered as random factors to control for repeated sampling.

I then ran a separate binomial GLMM (GLMM2) with a logit link function to examine, on a trial-by-trial basis, whether subjects performed better on trials that included objects they had previously chosen to explore with relevant behaviours, and whether this covaried with species. Trial outcome (correct vs. incorrect) was entered as the binary target variable into the model. Fixed factors entered into the model were i) experience with the objects (no relevant behaviour directed towards either object, relevant behaviour directed towards the functional object, relevant behaviour directed towards the non-functional object or relevant behaviour directed towards both objects), ii) species and iii) the interaction between species and prior experience (N=250; ten data points per individual per set, N= 13 subjects total from the block set and 12 subjects total from the rope set). Individual and object set were entered as random factors to control for repeated sampling.

Do birds alter their exploration to gain information about objects?

To determine whether individuals changed their behaviour depending on condition (pre- or post-tool-use training) and whether this differed depending on species, three separate GLMMS (3-5) were run, each featuring condition (pre- or post-tool-use training) and species as fixed factors, and individual and object set as random factors. The target variables for each GLMM were i) the proportion of trial time spent exploring all objects (GLMM3), ii) the proportion of time spent exploring functional objects (GLMM4), and iii) the proportion of trial time engaged in relevant behaviours (see Table 9 for examples; GLMM5). All proportional data were transformed for normality using the arcsine squareroot transformation (Crawley 2011, p248), and all GLMMs were run using a normal probability distribution and identity link function. Each individual had two data points per object set entered into the model (one for pre and one for post), resulting in 50 data points in total.

Results

Do birds learn from their exploration?

Overall, four out of eleven individuals performed above chance in the test trials (9 or more of 10 trials correct, binomial test with test probability of 0.5: $p = 0.021$), and only for the rope set. As a group, individuals' average test performance for both sets was above chance (Figure 12), but not significantly so (one-sample Wilcoxon test: $p = 0.079$). GLMM1 revealed that there were no significant between-species differences in performance on the test trials ($F_{1,21} = 0.065$, coefficient = -0.162 $\pm$ 0.632, $p = 0.801$, $r = 0.06$), and that performance on the test trials was not predicted by the total proportion of time that individuals spent exploring objects ($F_{1,21} = 0.184$, coefficient = 1.185 $\pm$ 2.763, $p = 0.673$, $r = 0.09$) or the proportion of time that subjects spent directing relevant behaviours towards the objects ($F_{1,21} = 1.399$, coefficient = -3.422 ± 2.893, p = 0.250, r = 0.25). The random factors subject (Z = 1.538, p = 0.124) and object set (Z = 0.452, p = 0.651) did not significantly predict test scores.

When examining performance on each individual trial, prior experience with the exact objects used in a test trial did not predict whether subjects chose correctly on that trial ($F_{3,242}$ = 0.035, p = 0.991, r = 0.01). Similarly, there was no significant interaction between species and prior experience with the objects on whether individuals chose correctly ($F_{3,242}$ = 0.393, p = 0.758, r = 0.04). The estimated variance for the random effect of object set was zero, and the remaining random factor subject (Z = 1.566, p = 0.117) did not predict a significant amount of variation.

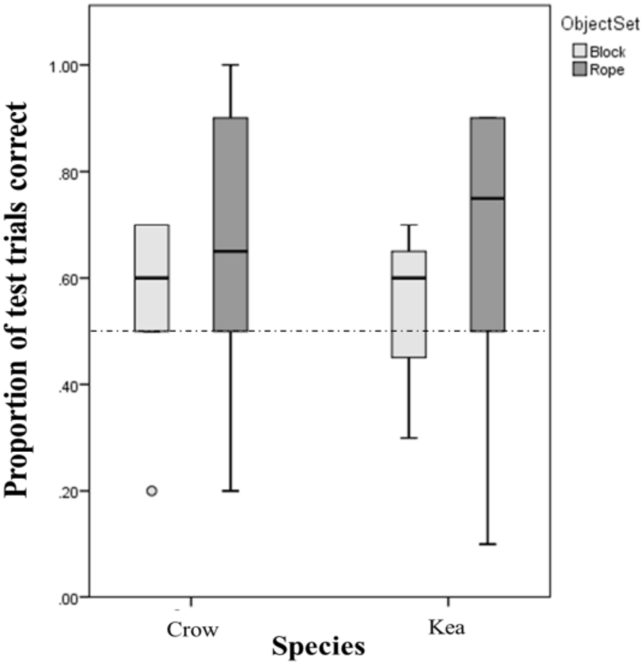

Figure 12. Boxplots illustrating the proportion of correct trials scored on either the block or rope set. Minimum and maximum values, median and 25th and 75th percentiles are shown. Dotted line denotes chance performance at 50%.

Species differences in exploration

There was a significant difference between species in the amount of time spent exploring the objects, with kea spending a significantly greater proportion of trial time interacting with the objects than the crows (kea: mean = 26% ± 6%; crows:

mean = 3% ± 2%; Figure 13; Table 10). Similarly, the kea spent a significantly greater proportion of trial time engaging in relevant behaviours (kea: mean = 16% ± 4%; crows: mean = 4% ± 1%), although it is notable that crows appeared to spend a large proportion of the total exploration time performing relevant behaviours (Figure 13). Kea also spent a significantly greater proportion of their exploratory time interacting with the functional objects relative to non-functional objects (kea: mean = 50% ± 6%; crows: mean = 27% ± 3%; Figure 14) than the crows. Although it was not possible to analyse statistically due to small sample sizes, sub-adult individuals (defined here as any bird that has not reached sexual maturity) from both species spent, on average, a greater proportion of trial time exploring the objects than adult birds (one kea sub-adult vs. seven adults: 49% vs. 22%; three crow sub-adults vs three adults: 5% vs. 0.4%).

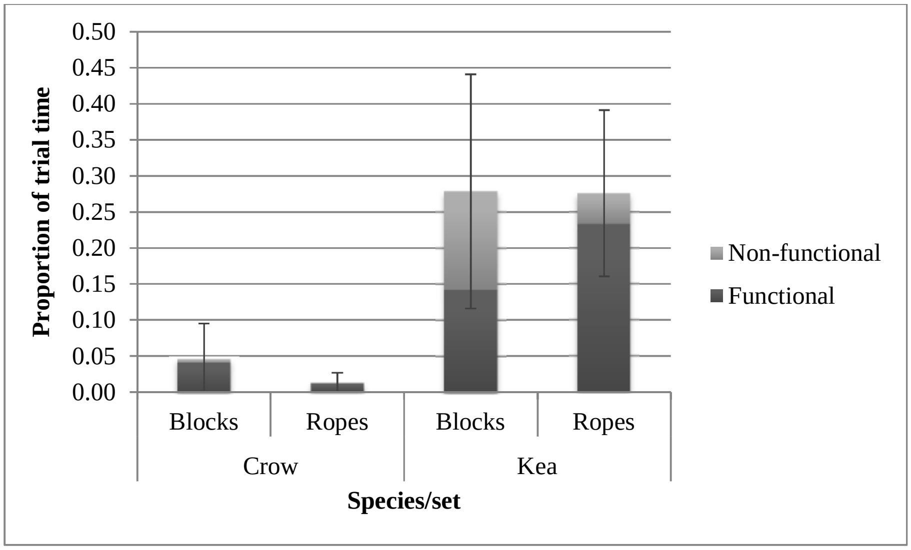

Figure 13. Species differences in exploration. Bar chart illustrating the average proportion of trial time that each species interacted with the block and rope sets, and the proportion of this time spent engaged in behaviours that could provide information about the object's function (i.e., relevant behaviours). Error bars denote bootstrapped 95% confidence intervals for the proportion of all exploratory behaviours (including relevant).

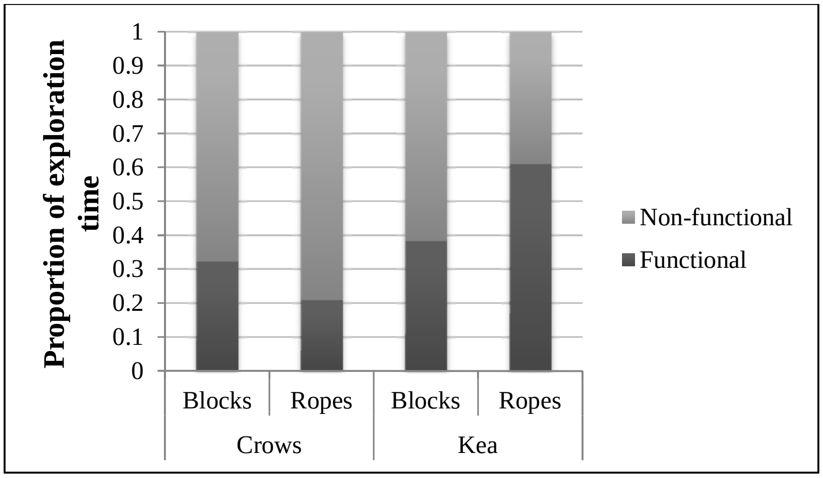

Figure 14. Proportion of time interacting with different object types. Bars illustrate the average proportion of exploration time (pre- and post-exploration grouped) individuals spent interacting with functional and non-functional objects.

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Table 10. Results from GLMMs 3, 4 and 5 (N= 50 data points from 13 individuals for each model). Full models are reported. Test statistics (F-statistic for fixed factors and Z value for random factors; significant results in bold), coefficients ± standard error and effect sizes are shown. Note that in each model, the estimated variance of the random effect 'object set' was zero, and is therefore not included in the table.

DV	IV	*F(Z)*	df1	df2	Coefficient	p-value	*R*
3. Exploration time	**Species**	**26.509**	**1**	**46**	**-0.455 ± 0.099**	**0.000**	**.60**
	Pre or Post	0.549	1	46	-0.059 ± 0.072	0.462	.11
	Species*PrePost	0.153	1	46	0.041 ± 0.697	0.697	.06
	ID (random factor)	1.405				0.160	
4. Exploring functional objects	**Species**	**4. 511**	**1**	**46**	**-0.457 ± 0.173**	**0.039**	**.30**
	Pre or Post	0.199	1	46	-0.107 ± 0.130	0.658	.07
	Species*PrePost	2.503	1	46	0.297 ± 0.188	0.120	.23
	ID (random factor)	1.415				0.157	
5. Relevant exploration	**Species**	**21. 562**	**1**	**46**	**-0.280 ± 0.083**	**0.000**	**.56**
	Pre or Post	0.044	1	46	0.039 ± 0.069	0.834	.03
	Species*PrePost	0.324	1	46	-0.056 ± 0.099	0.572	.08
	ID (random factor)	0.951				0.342	

Pre vs. post exploration

Each individual's exploratory behaviour for Phases 1 and 3 is summarized in Table 11. There was no significant difference in the proportion of trial time that subjects spent exploring the objects before or after encountering the tool use task (Figure 15,

Table 11). Similarly, there was no significant difference in the proportion of time subjects interacted with functional objects before and after the tool use task (Figure 16), or spent engaged in relevant behaviours (Figure 17). The overall proportion of time spent exploring, engaged in relevant behaviours or exploring functional objects was also not predicted by an interaction between condition and species (see Table 10).

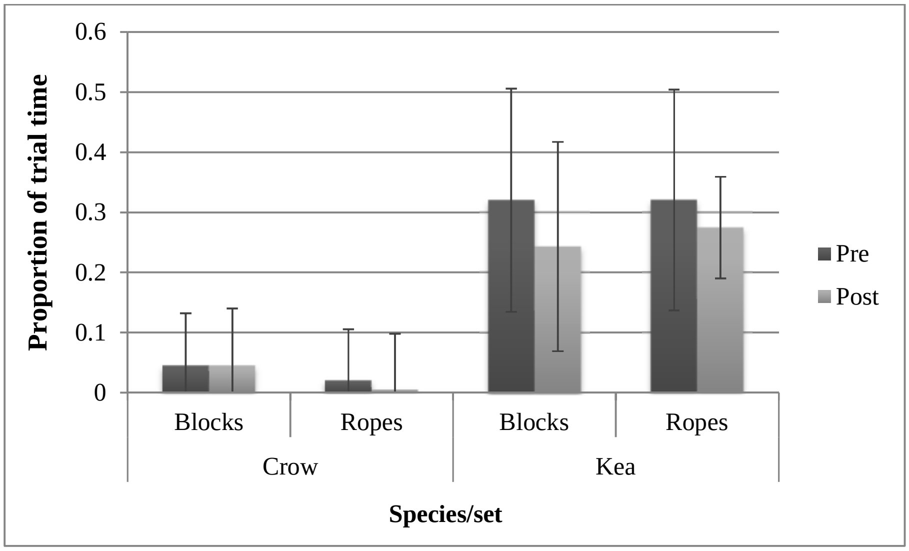

Figure 15. Proportion of trial time spent exploring objects in each exploratory condition. Average proportion of trial time both species spent exploring objects within each set either before (pre) or after (post) encountering the tool use task. Error bars denote bootstrapped 95% confidence intervals.

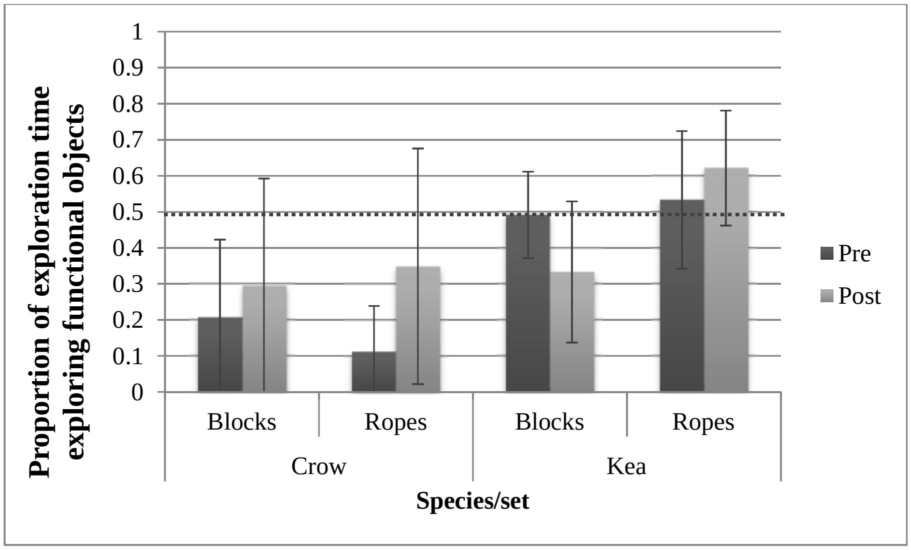

Figure 16. Exploration of functional objects pre- and post-training. Proportion of exploration time directed toward functional objects within each set either before or after encountering tool use task. Dotted line denotes 50% chance; Error bars denote bootstrapped 95% confidence intervals.

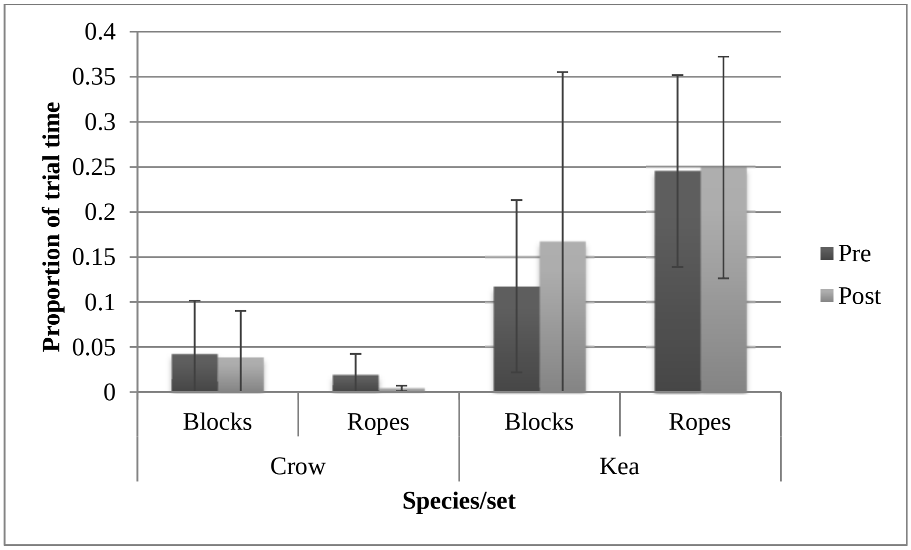

Figure 17. Relevant behaviours directed towards objects pre- and post- training. Average proportion of trial time both species spent engaged in relevant behaviours for each set either before or after encountering tool use task. Error bars denote bootstrapped 95% confidence intervals.

Table 11. Individual performance for test trials and exploration phases within each object set. Boxes show the number of objects of each type (functional or non-functional) contacted before the tool use task (grey) or after (diagonal stripes). For example, PI interacted with seven ropes (four functional, and three non-functional) before the training, and 10 ropes (5 of each type) after the training; JO interacted with 2 blocks (both functional) before the training and 2 blocks (one functional, one non-functional) after the training. Sub-adult individuals are italicized. Significantly above chance performance is marked with an asterisk*, and significantly below chance performance is marked with a †.

Species	ID	Set	Correct (of 10)	Functional					Non-functional				
Kea	PI	Rope	1†	▩	▩	▩	▩	▨	▩	▩	▩	▨	▨
		Block	6	▩	▩	▩	▨		▩	▩	▩		
	PA	Rope	9*	▩	▩	▩	▩	▩	▩	▩	▩	▩	▩
		Block	7	▩	▨	▨	▨		▩	▩	▩	▨	▨
	FR	Rope	9*	▩	▩	▩	▩		▩	▩	▒		
		Block	6	▩	▩	▒	▒	▒	▩	▩	▩	▩	▩
	KE	Rope	5	▩	▩	▨	▨		▩	▩	▩	▩	
		Block	5	▩	▩	▩	▒	▒	▩	▩	▩	▒	
	LI	Rope	7	▩	▨	▨	▨		▩	▩	▩	▨	
		Block	7	▩	▩	▩	▩		▩	▩	▨		
	AN	Rope	8	▩	▩	▩	▩	▩	▩	▩	▩	▩	▨
	JN	Block	3	▩	▩	▨	▨	▨	▩	▩	▩	▩	▨
	RO	Block	4	▩	▩	▩	▩	▩	▩	▩	▩	▩	▨
Crow	*BL*	Rope	5	▩	▩	▩	▨		▩	▨			
		Block	2	▩	▩	▩	▩	▨	▩	▩	▩	▨	▨
	JO	Rope	7	▒					▨				
		Block	7	▩	▒				▨				
	ST	Rope	2										
		Block	6	▨	▨	▨			▨	▨	▨	▨	▨
	AT	Rope	10*	▒	▒				▩				
		Block	7	▩	▩	▒	▒		▒	▒	▒		
	EM	Rope	6	▨					▨	▨			
		Block	6						▒	▒			
	AZ	Rope	9*	▨	▨				▩	▨			
		Block	5	▒	▒	▒			▒	▒			

Experiment 2: Block set- colour versus pattern as a relevant feature.

The results from Experiment 1 showed that four individuals performed significantly above chance in selecting functional objects to solve problems on the rope set, but not on the block set. This difference in performance could be linked to the materials themselves by reflecting a better understanding of rigidity, which unlike weight, is visible following manipulation and in this case also represents more of a binary structural property (objects are either rigid or flexible) relative to weight, which occurs along a continuum. Alternatively, it could be linked to the salience of the objects' visual features (e.g., colour relative to pattern). Colour in particular has been shown to be a highly salient stimulus, both in natural and in experimental contexts (Guilford 1990; Moller & Erritzoe 2010; Kazemi *et al.* 2014). If colour was a more salient feature associated with structure, subjects were expected to perform better on this set of test trials relative to the block set in Experiment 1.

Procedure

This was tested by presenting subjects with a new block set using a similar procedure to Experiment 1, but this time with colour as the relevant feature associated with weight, and pattern as an irrelevant feature. Colours and patterns that the birds had not previously encountered in Experiment 1 were used. As the birds had already learned that the blocks could be used in a problem-solving task in Experiment 1, they received only post-training exploration sessions with the baited apparatus in full view. Each subject was given up to 4 sessions in which they were required to interact with three exemplars of each object type (functional and non-functional) before completing ten test trials.

Analysis

Subjects' proportion of correct trials was compared to their proportion of correct trials for the block set in Experiment 1 using a Wilcoxon signed-rank test, with a significance level of $p < 0.05$. The exact p-value is reported.

Results

While no subjects performed above chance for the weight set when the relevant feature was pattern, three kea (PA, PI and RO) and one crow (AZ) performed above chance when the relevant feature was switched to colour. Two of these individuals (PA and AZ) had also performed above chance for the rope set. Nonetheless, at a group level, performance was not significantly better when colour rather than pattern was the relevant feature on the blocks (Wilcoxon signed-rank test, N = 11, Z = -0.358, *p* = 0.738, *r* = 0.07).

Experiment 3: No exploration control

Procedure

The results of Experiments 1 and 2 suggest that some kea and crows are able to select functional objects significantly above chance levels after an exploration phase, and particularly when colour is associated with functionality. In order to ascertain whether these individuals are succeeding due to information gained during exploration it is important to test an alternative explanation, which is that subjects may be able to rapidly learn the reward contingencies in the test trials. To measure how well subjects would perform on test trials without any prior exploration of the objects, subjects were presented with a novel object set with novel relevant (colour) and irrelevant (pattern) features and were presented with 10 test trials in which they could choose between an unfamiliar functional or non-functional object to solve the task. In order to be conservative, I matched the control set to the exploration set on which the greatest number of individuals within each species performed significantly above chance. For the kea, this was the block set from Experiment 2 (3/6 individuals significantly above chance; colour relevant feature) and for the crows, this was the rope set from Experiment 1 (2/6 individuals above chance; colour relevant feature).

If exploration facilitated learning about the objects' functionality and thus enabled subjects to perform well on test trials in Experiments 1 and 2, it is expected that subjects that performed significantly above chance on test trials following exploration would perform at chance levels in this experiment. In contrast, if subjects performed above chance in this condition as well as previous test trials, this would suggest that either: i) subjects may have generalized the rule that they learned during their exploration and applied it to these trials (e.g., colour correlates with functionality) or ii) are able to rapidly associate success with the visual properties of the objects, without any understanding of functionality. Overall it was predicted that if exploration enabled learning about object structure, performance of the group should be better on test trials following exploration than no exploration.

Analysis

To compare subjects' performance on test trials following exploration or no-exploration, a GLMM with a binomial probability distribution and a logit link function was run featuring the proportion of correct trials as the target variable, condition (exploration versus no exploration), species, and the interaction between condition and species as binary fixed factors, and subject as a random factor. Each individual had one data point per object set entered into the model, resulting in 22 data points total in the model (N=11 individuals).

Results

All five subjects that performed significantly above chance after exploring the objects performed at chance levels in this experiment (Table 12). One subject which did not perform significantly above chance in any test sessions in Experiments 1 and 2 did so for this experiment. Performance on test trials was significantly predicted by condition, with subjects showing higher performance in conditions in which they could explore the objects beforehand compared to the no-exploration control condition ($F_{1,18} = 10.465$, coefficient = -1.015 ± 0.405, $p = 0.005$, $r = 0.60$; see Table 12 for individual scores in each condition). There was no significant between-species difference in scores for either condition ($F_{1,18} = 0.037$, coefficient = 0.049 ± 0.625, $p = 0.938$, $r = 0.05$), or interaction between species and condition ($F_{1,18} = 0.032$, coefficient = 0.107 ± 0.595, $p = 0.860$, $r = 0.08$). There was no significant effect of subject as a random factor ($Z = 1.388$, $p = 0.165$).

Table 12. Individual scores for test trials after subjects were allowed to explore the objects (Experiment 2 for kea and Experiment 1 ropes for crow) or not (no exploration column). Bold denotes above chance performance.

Species	**Subject**	**Proportion of correct trials**	
		Exploration	**No exploration**
Kea	PA	**1.00**	0.80
	PI	**0.90**	0.20
	FR	0.60	0.10
	LI	0.40	0.50
	RO	**0.90**	0.80
	JN	0.50	0.60
Crow	BL	0.50	0.50
	AZ	**0.90**	0.40
	JO	0.70	**0.90**
	AT	**1.00**	0.40
	EM	0.60	0.50
	MEAN	0.73	0.51
	SD	0.21	0.23

General Discussion

Overall, six birds performed significantly above chance on test trials in Experiments 1 and 2 when they could explore the objects beforehand (two for the rope set in Experiment 1, two for Experiment 2 and two for both). Furthermore, all of these individuals performed at chance levels on test trials using similar visual cues, but in which they had no opportunity to explore the objects (Experiment 3). Five of these individuals encountered a no-exploration task that was directly comparable to the one in which they performed significantly above chance with exploration, providing support for the idea that exploration facilitated learning about the structural properties of the objects that informed test performance. One individual (FR) was significantly above chance for the rope set, and at chance levels for the control block set. Although colour remained the functional feature in both of these object sets, the structural properties of the two object sets were different, so his data, although suggestive cannot be interpreted in a comparable way to the other five birds.

It is also notable that one individual performed significantly above chance in Experiment 3, showing individuals can learn within 10 trials which objects are functional in the absence of exploration. It is uncertain whether this individual demonstrated rapid contingency learning in the absence of any understanding of functionality, or whether he may have generalized a rule (e.g., colour correlates with functionality) learned during his exploration and 20 previous colour-relevant test trials and applied it to these trials. It is also possible that some birds may have succeeded through adherence to a bias for a certain visual feature (e.g., colour) with little understanding of the task. For example, at least one bird (PI) showed a strong colour bias in the rope exploration condition that was resistant to contingency learning in the 10 test trials, with the bird choosing the incorrect object in 9/10 trials. Nonetheless, a comparison of all subjects' performance on exploration compared to no-exploration test trials revealed a significant effect of condition, with birds performing better in test sessions when they had previously explored the objects. When the individual and group level results are taken together, they provide preliminary evidence that experience manipulating objects in an unrewarded context improves both kea and New Caledonian crows' performance on a later task in which the objects could be used as tools.

During test trials following exploration, subject's performance on a trial-by-trial basis was not predicted by whether they had previously interacted with those particular objects presented in that trial, suggesting that individuals may instead have formed some general concept about the objects' structural properties based on their relevant visual feature. That subjects only performed significantly above chance when structure was associated with colour suggests that in the absence of causally relevant cues such as size or shape, colour, which has a high degree of ecological relevance, may serve as a more salient feature for forming these associations (Guilford 1990; Moller & Erritzoe 2010).

Although exploration appears to play a role in learning about functional properties, it remains unclear what aspects of exploration drive this learning. In Experiment 1, performance in the problem-solving task was not predicted by the quality or quantity of experience that individuals had with the objects. These results are perhaps most similar to those of Manrique *et al.* (2010; 2011) which show that capuchins and great apes are more likely to choose functional tools to solve a task if they had previous experience with those objects, and that this performance was not predicted by the quality of information provided (in terms of exploring the objects themselves or watching demonstrations by an experimenter).

Both kea and New Caledonian crows did not appear to change their exploratory tactics after encountering the tool-using task, suggesting that their exploration was not driven by an attempt to gain information about the objects. Specifically, there was no difference in the amount of time that subjects spent exploring the objects, the proportion of relevant behaviours directed toward the objects or the type of objects (functional or non-functional) explored after encountering the tool use task. This was the case despite the baited apparatus being in full view, and even after subjects had completed their first object sets and had learned that the objects they were presented with could later be used as tools during the test trials. These results are consistent with those of Povinelli & Dunphy-Lelii (2001), which show that chimpanzees do not engage in exploration in order to gain information about objects that are visually identical but different in underlying structure/functionality.

Although few other studies have explicitly examined whether nonhuman animals adjust their exploration in contexts that provide an opportunity to learn about physical affordances compared with those that do not, the performance of both the kea and the crows contrasts with the behaviour of wild capuchins, which alter their manipulation of potential stone tools in order to gain information about the stone's weight in the absence of obvious visual cues such as size (Visalberghi *et al.* 2009). Similarly, when young children are faced with a causally ambiguous stimulus, such as a box with two potential levers which can be pushed to make a toy appear, they will increase their exploration of this stimulus relative to a non-ambiguous stimulus such as a box with only one lever (Schulz & Bonawitz 2007). Unlike the capuchin study, object exploration in this study did not take place within an immediate goal-directed context where individuals manipulated objects so that they could choose an appropriate tool. Instead, the birds would have needed to anticipate that they would be allowed to use the objects as tools following an exploration session, which may have posed a cognitive constraint for these subjects.

Kea spent significantly more time interacting with the objects during the exploration phases, both overall and in terms of relevant exploration, than the crows.

These differences are consistent with each species' behaviour: whereas corvids are typically neophobic, kea are well-known for their pronounced neophilia and object play that persists into adulthood. This is contrary to the general trend that species which habitually use tools in the wild generally show more frequent and complex object exploration than non-tool-using species; however, these differences may have additionally been exaggerated by the groups' respective histories. Whereas the kea had been born and raised in a captive environment and habituated to experimental contexts from a young age, the crows were wild-caught and presumably had minimal close contact with manmade objects. Stress caused by a sudden transition to captive environments may affect cognitive functions by either disrupting or facilitating memory processes depending on the level of stress, or by causing lapses in attention (reviewed in Mendl 1997). Although measures were taken to ensure the crows were fully habituated to both their captive environment and the test objects before beginning exploration trials, the crows may still have had little motivation to interact with the objects, whereas the kea are often rewarded in experiments for doing so. Although the sample size in the current study (N = 6 crows) was too small to examine any effects of neophobia on test performance, future studies using larger sample sizes should include individual variation in neophobia as a factor to determine whether this might have impacted performance in the test trials. Despite this difference in exploration between species, there was no significant difference between the performances of kea or New Caledonian crows on the test trials.

The sample of 14 birds included four sub-adults (one kea and three crows). Although the limited number of sub-adult birds precludes statistical comparisons, these birds showed, on average, higher rates of exploration than their species average. Additionally, of the four birds that performed above chance in test trials for Experiment 1, three of these individuals were sub-adults. This suggests that perhaps there is a critical developmental stage during which individuals attend to and learn from stimuli in their environment, particularly when the costs of doing so are lower than in adulthood.

In terms of ultimate mechanisms, these results support the hypothesis that unrewarded object exploration functions to provide information about object properties which can then be used to solve problems, but do not rule out other potentially overlapping functions of exploration such as honing manual skills or generating novel behavioural sequences (Power 2000). Given its apparent costliness it is likely that exploration confers myriad benefits (Bateson & Martin 2013). Further research explicitly addressing each of these benefits and their relative importance is needed to gain a richer view about how different animals learn about and interact with their environments (see Renner 1990 for a discussion).

In summary, this study provides preliminary evidence that kea or New Caledonian crows apply information generated from their exploration of novel objects to select functional tools in a later problem-solving task, however they do not seem to engage in strategic exploration to gain information about the functional properties of objects once familiar with the problem-solving task. These data ultimately support the hypothesis that a key function of exploration in these birds is to provide opportunities to learn about object properties, however further data are needed from more experimental contexts to confirm this, as well as to test other alternative (but not mutually exclusive) hypotheses.

Chapter 6. Prosocial Behaviour in Captive Ravens

The data presented in this chapter have been submitted for publication and are currently under review:

Lambert, M.L., Massen, J.J.M., Seed, A.M., Bugnyar, T. and Slocombe, K.E. (*under review).* An 'unkindness' of ravens? Measuring prosociality in *Corvus corax. Animal Behaviour.*

Abstract

In addition to solving physical problems, complex cognition may allow individuals to deal with the challenges of social living, and in particular the maintenance of strong affiliative relationships with group members, which are typically characterized by prosocial behaviours such as grooming and agonistic support. In recent years there has been considerable research effort to determine whether other species exhibit prosocial motivations parallel to those of humans; however these studies have focused primarily on primates, and with mixed results. For this study, captive ravens were presented with a modified prosocial choice task that addresses several criticisms of previous methods by including a stringent pre-training regime and a setup that disentangles motivation to provision a conspecific from motivation to feed next to one. In this task subjects (N = 6) received no rewards for themselves but could choose to deliver food rewards to either a conspecific or an empty, inaccessible compartment. Subjects did not demonstrate any prosocial tendencies (i.e., they did not preferentially choose to reward a conspecific over the empty compartment), and instead often ceased pulling on test trials when they received nothing for themselves. The relationship between the subject and the partner had no influence on the subject's choices; however subjects were more likely to pull immediately following attention-getting behaviours by the partner, and immediately after displaying themselves. These results contribute to a growing body of evidence that despite their sophisticated social cognitive abilities and range of cooperative behaviours exhibited in the wild, un-paired (or unbonded) ravens do not act to benefit conspecifics in the absence of immediate self-gain.

Introduction

Humans' extreme prosocial, or 'other-regarding' behaviour, is unparalleled in nature and is often cited as a defining characteristic of humanity that facilitates human cooperation on a global scale and may have played a key role in the evolution of our complex culture and technology (Fehr & Fischbacher 2003). Despite its significance, the questions of whether humans alone possess intrinsic prosocial motivations, and how our unique levels of prosociality evolved have historically remained unanswered. In recent years, however, these topics have become the centre of much empirical focus and theoretical debate (Burkart *et al.* 2009; Burkart & van Schaik 2010; Silk & House 2011; Thornton & McAuliffe 2015; Burkart & van Schaik 2016)

Examples of prosocial behaviour can ostensibly be found throughout the animal kingdom, but the question remains as to whether, on a proximate level, these behaviours are governed by the same underlying psychological mechanisms (i.e., other-regarding concern) as those that prompt many human prosocial behaviours (de Waal & Suchak 2010; Jensen *et al.* 2014). Recent research has aimed at probing the motivational mechanisms underpinning prosociality in other species, yet this has proved difficult to test. For example, Ben-Ami Bartal and colleagues (2011) report that rats behave prosocially toward conspecifics due to an empathetic concern for their welfare, as evidenced by their willingness to free a conspecific trapped in a restraining tube. This was later refuted, however, by a lower-level explanation that subjects were motivated by a desire for social contact rather than empathy, in part because subjects continued to press the release lever which opened the restraining tube even after conspecifics had been freed (Silberberg *et al.* 2013). Additionally, subjects showed few release responses in an early condition in which the trapped individual was freed into an adjacent compartment which the subject could not access, and increased responses once the conspecific was instead released into their own compartment, highlighting the need for strict behavioural controls when inferring particular cognitive processes.

In the last decade there has been a surge of research aimed at investigating prosociality in nonhuman animals in controlled laboratory settings in order to tease apart these factors. One of the most widely used paradigms for measuring prosocial tendencies in other species is the prosocial choice task (Silk *et al.* 2005; see Figure 18 for a schematic of the setup), a provisioning paradigm where subjects may choose between two options, one of which delivers food to both the subject and a nearby conspecific (prosocial choice; often denoted as the 1/1 option with payoffs for the donor and recipient, respectively) and the other which provides food to only the subject (selfish choice; 1/0 option). Reward distributions may also be manipulated so that subjects do not receive any rewards for either choice but rather may incur a slight energetic cost for pulling to donate food to a recipient (0/1 option), or must forgo a qualitatively better reward for a less-preferred reward in order to also benefit their partner (HQ-0 vs. LQ-HQ: Sterck *et al.* 2015)[3]. To further examine the motivations behind prosociality, many researchers have focussed on the inter-individual differences in prosocial tendencies based on the relationship between the subject and the partner. In all cases, prosocially motivated subjects are expected to preferentially choose the option which benefits a conspecific at little or no cost to themselves.

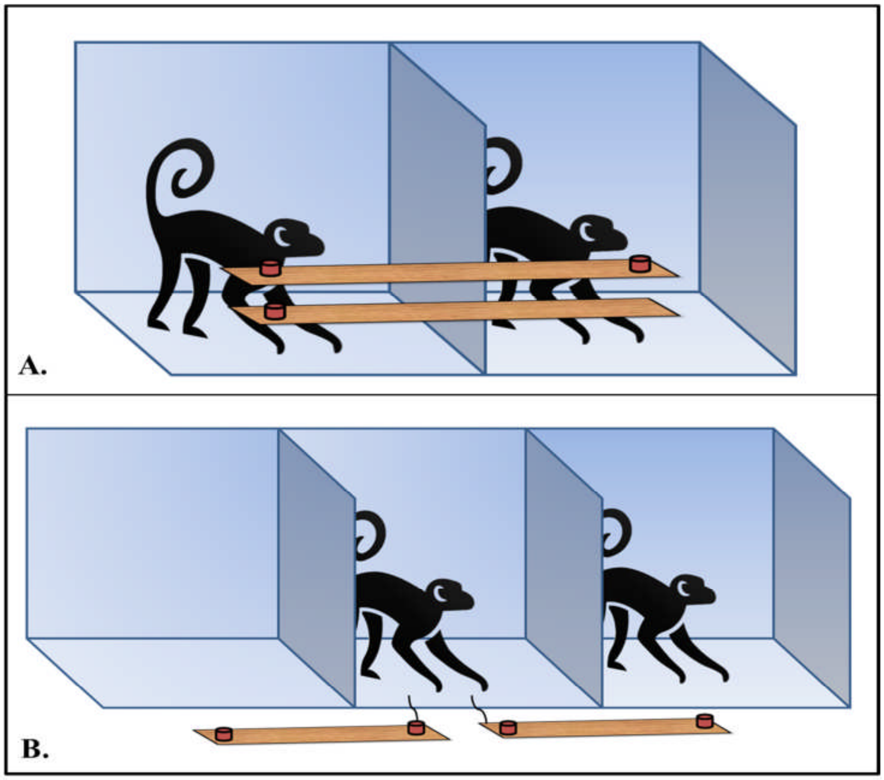

Figure 18. Two common versions of the prosocial choice task (PCT). In both tasks, subjects choose one of two trays, one of which also provides benefits to a partner. A)

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[3] Note that although subjects may incur an immediate cost in (0/1) paradigms for acting to provision a partner, subjects may still experience later benefits in terms of reciprocal altruism or kin selection, as discussed in Chapter 3.

Two-compartment setup with two vertically aligned trays. B) Three-compartment setup with two horizontal trays.

Several variations of the prosocial choice task have been used with a range of nonhuman species, with most available data coming from the primate order, and with equivocal results. While some studies have reported other-regarding preferences in several primate species (chimpanzees: Horner *et al.* 2011; capuchins: Lakshminarayanan & Santos 2008, Takimoto *et al.* 2010; macaques: Massen *et al.* 2010; marmosets: Burkart *et al.* 2007, Mustoe *et al.* 2015; tamarins: Hauser *et al.* 2003, Cronin *et al.* 2010) other studies with the same species, and in some cases the same individuals, have found contrasting results (chimpanzees: Silk *et al.* 2005, Jensen *et al.* 2006, Vonk *et al.* 2008, Yamamoto & Tanaka 2010; capuchins: Burkart & Van Schaik 2012; macaques: Burkart & Van Schaik 2012; tamarins: Cronin *et al.* 2009, Stevens 2010).

These differences have been attributed to various contextual factors and methodological differences between studies including the visibility of food rewards, the relationship between the subject and the recipient and the subjects' understanding of the task (Cronin 2012; Burkart & Rueth 2013). For example, when confronted with the same paradigm used with primates, pre-school age children fail to show prosociality in a cost-free (1/1) version of the task, but are prosocial in a costly (0/1) version – a finding that has been attributed to the higher attentional demands of the cost-free version rather than a lack of prosociality (Burkart & Rueth 2013). Prosocial behaviour may additionally be dependent on the ability to appreciate others' goals or needs, and may thus only be expressed in response to signs of need by the recipient (Vonk *et al.* 2008; Horner *et al.* 2011; Cronin 2012; Schwab *et al.* 2012). A few studies have examined the effect of the recipient's behaviour on the subject's choices to determine whether direct requests or expression of interest in the reward affect the likelihood of prosocial choices by subjects. Those that have, have provided mixed results with reports of cottontop tamarins and chimpanzees being less likely to choose the prosocial option on trials where their partner reached out for the reward (Cronin *et al.* 2009) or produced begging gestures (Horner *et al.* 2011). In contrast, other studies have reported begging gestures to have no effect on chimpanzee subject choices (Vonk *et al.* 2008), whilst general attention getting behaviours by the partner such as food grunts or hitting the caging had a positive effect on prosocial choices (Horner *et al.* 2011).

Recently, Tan *et al.* (2015) and Marshall-Pescini *et al.* (2016) highlighted several methodological limitations with the current paradigms used to test prosocial preferences in nonhuman animals. One of the primary limitations faced by existing studies is that very few (Tan *et al.* calculated 40.9%) include the necessary pre-test to ensure that subjects understand the test setup, and those that do may not be adequately counterbalanced to prevent location biases that may arise from pretraining. For example some studies include a phase in the beginning where subjects are first allowed to interact with the apparatus and pull the trays in order to learn the contingencies of the task, in some cases in as few as 10 trials (de Waal *et al.* 2008; Amici *et al.* 2012), but do not test whether subjects actually understand these contingencies. Tasks which do require subjects to meet a pre-test criterion for understanding of the task may face a different problem, which is overtraining. Most studies of prosociality are conceptually similar to the two-compartment setup (see Figure 18a), such that during this pre-training subjects are continually rewarded for choosing the tray which delivers food to the neighbouring compartment, which may carry over into the test phase and consequently make it difficult to disentangle prosocial preferences from training biases (Burkart *et al.* 2007; Lakshminarayanan & Santos 2008; Cronin *et al.* 2009).

Other studies have used setups involving three compartments (see Figure 18b) which would overcome any biases that arise in a pre-training condition, however these setups usually feature two horizontally aligned trays which deliver food to each of the side compartments. The subject is present in the middle and can therefore choose one of the side trays to provision the partner’s compartment or an empty compartment. Unfortunately these studies introduce a new potential confound of side biases, in which the subject may prefer to spend time close to or away from their partner in the neighbouring compartment, in which case they may simply pull the tray which is closest to them at that moment (Jensen *et al.* 2006; Tan *et al.* 2015; Marshall-Pescini *et al.* 2016). Consequently, rather than providing evidence for or against prosociality, positive or negative results may instead be attributed to social factors or a lack of understanding. In order to rule out these confounds in the future a number of methodological changes have been suggested including a strict self-regard pre-test and counterbalancing to avoid location biases (Tan *et al.* 2015; Marshall-Pescini *et al.* 2016).

The discrepancies and methodological weaknesses present in the current literature highlight the need to explore this topic further not only by using consistent methodology between species (e.g., Burkart *et al.* 2014) that addresses the weaknesses in the standard paradigms used, but also by using multiple tasks with the same species (and subjects where possible) before drawing general conclusions on the presence or absence of a particular predisposition (Kim *et al.* 2015; Tan *et al.* 2015; Marshall-Pescini *et al.* 2016). Additionally, research with other species outside of the primate order is needed in order to gain a broader understanding of the various factors that may give rise to prosocial behaviour such as breeding system, cognitive ability and social tolerance.

Corvids are frequently cited alongside primates for their complex social cognitive abilities (Emery & Clayton 2004; Seed *et al.* 2009a). Among corvids, ravens in particular are known for their social complexity; during ontogeny they form large, non-breeder flocks during which time they must keep track of the identities of and relationships between conspecifics, while additionally forming their own strong social bonds (Heinrich 2007; Braun & Bugnyar 2012). Ravens have shown remarkable long-term memory for these former group members by responding differently to the calls of familiar or unfamiliar individuals, or previously affiliated or non-affiliated individuals, after periods of up to three years (Boeckle & Bugnyar 2012). In addition to tracking social information, ravens have also demonstrated Theory-of-Mind-like skills by strategically adjusting both their food caching and pilfering behaviour according to the visual perspectives and inferred presence of conspecifics (Bugnyar 2011; Bugnyar *et al.* 2016).

Outside of these competitive contexts, ravens also show a range of seemingly cooperative behaviours, both in the wild and in captivity, which make them an interesting model for investigating prosociality. In the wild, upon encountering a large food source, ravens vocalize to recruit conspecifics rather than feeding alone (Heinrich 1988), and during conflicts provide agonistic support to close affiliates (Fraser & Bugnyar 2012), or console close affiliates after conflicts (Fraser & Bugnyar 2010). In captivity, subjects can learn to cooperate in a loose-string task in which two birds must simultaneously pull a string to bring in a tray holding a reward, and this successful cooperation increases among birds with higher levels of social tolerance between them (Massen *et al.* 2015b).

Recently, several versions of the prosocial choice task have been used with ravens and other corvid species, with results that mirror some chimpanzee studies. Using a setup similar to that used with chimpanzees (Silk *et al.* 2005), Di Lascio *et al.* (2013) allowed captive ravens to open one of two boxes, allowing access to food rewards for either themselves and a partner in a neighbouring compartment, or only themselves. The authors found no evidence for prosociality; importantly, however this may have been due to a lack of understanding the apparatus rather than indifference to the partner's payoffs. Using a slightly modified version of this paradigm, Schwab *et al.* (2012) found that jackdaws preferentially chose the reward option that simultaneously benefitted a conspecific, but primarily when the conspecific had already approached that option – a result that the authors attribute to stimulus/local enhancement rather than proactive prosociality. When presented with tokens that could only be exchanged by the partner for a reward, Massen *et al.* (2015a) found that subadult ravens generally preferred to cache the tokens rather than transferring them to conspecifics. Taken together these results suggest that some species of corvid are not proactively prosocial, however their performance may alternatively be explained by the peripheral demands of particular prosocial tasks. Convergent evidence from different paradigms is, therefore, needed to resolve tension between naturally occurring cooperative behaviours and inconclusive performance on experimental tasks to date.

For this study, a prosocial choice task was presented to the same group of ravens tested in Massen *et al.*'s (2015a) study (including two birds that did not participate in Massen *et al.*'s study) similar in design to that commonly used with primates. Several important modifications were made to the methods in order to overcome previously identified weaknesses in the paradigm (see methods and discussion). In this study, subadult ravens were paired with affiliate and non-affiliate partners in a paradigm in which subjects could choose between a tray that delivered food to a conspecific partner in a neighbouring compartment (0/1 option) or a tray that delivered food to an empty compartment (0/0 option). It was predicted that, if subjects were proactively prosocial, they would be willing to incur a small cost by pulling the tray which delivered food to a conspecific more often than they would pull the same tray in a non-social control condition; a trend which might be more likely to appear in affiliate dyads. Alternatively, if the birds were not prosocial, they were expected to pull either tray at random or to cease pulling when they did not receive any rewards for themselves.

Rather than acting as definitive evidence of a lack of prosociality in other species, negative results of previous studies may be attributed to several key methodological factors such as the complexity of the setup (see Horner *et al.* 2011 for discussion), failure to examine differences in affiliative relationships (e.g., Silk *et al*. 2005), confounds of social facilitation (e.g., Jensen *et al.* 2006) and the attentional demands of a food reward in front of the subject's compartment (Burkart & Rueth 2013). Several key features were incorporated into this test to address each of these potential issues by requiring subjects to pass an extensive pre-test for understanding of the apparatus, testing subjects with multiple partners of varying affiliation and using a setup that counters any potential social facilitation biases or distraction from visible food rewards in front of the subject's compartment. By systematically countering each of these alternatives, the most likely explanation for a negative result in this study is that the birds are indifferent to the gains of their partner.

Methods

Subjects and test site

Subjects came from a group of 12 hand-reared ravens. Nine of the birds participated in the study (subadults: 3 females and 4 males; adults: 1 male and 1 female): 1 as a subject only, 3 as partners only and 5 as both partners and subjects (counterbalanced between subject-first or partner first). The 3 birds who did not participate in the study were not willing to reliably enter the testing area of the enclosure and the three birds who only participated as partners were not comfortable in the central testing compartment required for subjects.

All subadult birds hatched in 2012, and the adult male and female hatched in 2011 and 2010, respectively (Table 13). All subjects were housed together as a single social group at the Haildhof Research Station in Bad Vöslau, Austria. Feedings occurred twice daily in the mornings and afternoons and consisted of a mixture of dairy items, meat, bread, vegetables and fruits. Birds had ad libitum access to water in both the home aviary and testing compartments.

Participation in training and testing sessions was voluntary. Ethical approval for this study was granted by the Department of Biology Ethics Committee, University of York, and by the ethical board of the behavioural research group at the faculty of Life sciences, University of Vienna (case number: 2015-003). Prior to this study the birds had participated in a number of physical and social cognitive experiments, including several studies on cooperative string pulling and prosociality (e.g., Massen *et al.* 2015a; Massen *et al.* 2015b); however, the setup for the current study was novel to the birds and took place in separate compartments from the previous studies.

Table 13. Detailed subject list including relatedness, sex, age at time of testing, rearing history and dominance rank. HR=hand-reared in captivity, PRW=parent-reared in the wild.

ID	Age	Sex	Kin group	Rearing	Rank
GE	2	M	1	HR	5
NB	2	F	1	HR	7
LO	2	F	1	HR	9
AD	2	F	2	HR	11
JO	4	F	3	HR	10
RY	3	M	4	PRW	8
HO	2	M	1	HR	3
TM	2	M	2	HR	2
LG	2	M	2	HR	1

Dyads

In order to investigate potential effects of recipient identity on prosocial preferences, each subject was paired with one of two partners, one of whom was an affiliate and the other a non-affiliate (see Table 14). These two partners were of opposite sex such that each bird was tested with a male and female partner (e.g., if the affiliate was male, the chosen non-affiliate was female, and vice versa). Across the 6 birds, equal numbers of female and male affiliates were used, meaning at a group level affiliation level with the partner was not confounded with sex of the partner. Thus, if sexual bonding affected prosocial behaviour, it was expected that matched-sex pairs would predict a greater amount of variation in prosocial behaviour, whereas if prosociality was influenced by nonsexual bonds, it was predicted that affiliation level would have an effect. Subject and partner roles were never reversed within dyads to prevent potential reciprocity biases. Affiliation levels between potential dyads were determined using long term social data as detailed in the section below.

Social data

Data on dominance and affiliation were collected to determine subject-partner dyads (affiliation data) and to examine whether differences in rank between the subject and the partner influenced subject choices during testing (dominance data).

Dominance

Dominance rank data were collected from monopolization experiments conducted during the time of the experiment, which consisted of presenting the group with two large pieces of partially frozen meat, a highly valued and easily monopolizable resource, for 30 minutes. All displacements during this time were recorded and later entered into a matrix with actors in rows and recipients in columns. Matman (version 1.1; de Vries et al. 1993) was used to calculate Landau's linearity indexes (h'). A significant linear hierarchy was identified throughout the study (h'= 0.581, N = 11, $p < 0.01$), based on 244 interactions and 18.18% of unknown relationships. These data were converted into relative rank difference scores for each dyad by subtracting the partner's rank (ranging from 1 to 11) from the subject's rank and using the value as an independent variable in the analyses. Rank difference scores ranged from -4 to 9.

Affiliation

Data on affiliative relationships were extracted from a database of ongoing focal observations taken from April to September 2014. During this time each individual was filmed for 5 continuous minutes, two to three times per week. Each individual's frequency of allopreening and contact sitting with all other individuals was coded from video observations, and this number was then normalized per individual by calculating a percentage of affiliative interactions per partner, or relationship quality score. When selecting dyads, affiliate partners were selected as those birds whose relationship quality score with the subject was greater than zero, meaning they engaged in affiliative behaviours (preening, contact sitting) with, and spent time in close proximity to the subject. Non-affiliates were selected as neutral birds (relationship quality score = 0) which did not have a particularly affiliative or agonistic relationship with the subject. For cases of less socialized, or lower-ranking birds (JO, RY), affiliates were chosen as those individuals who, based on the observation of the experimenters, had the least amount of agonistic interactions with the subject, also reflecting a relationship quality score of zero. Non-affiliates for these two birds were selected as those which, following affiliates, also had the least amount of agonistic interactions with the subject.

Table 14. Testing dyads for each subject including the affiliation, sex and relative rank difference of the partner. Partners are listed in order of testing for each subject. ♀: female; ♂: male.

Subject ID	Partner ID	Affiliation	Partner sex	Rank difference
NB♀	LG	Affiliate	M	6
	AD	Non-affiliate	F	-4
GE♂	LG	Non-affiliate	M	4
	NB	Affiliate	F	-2
JO♀	TM	Non-affiliate	M	8
	AD	Affiliate	F	-1
AD♀	TM	Affiliate	M	9
	LO	Non-affiliate	F	2
LO♀	HO	Affiliate	M	6
	JO	Non-affiliate	F	-1
RY♂	GE	Non-affiliate	M	3
	LO	Affiliate	F	-1

Setup and apparatus

Training and testing took place in an outdoor compartment attached to the home aviary (7 x 1.7m). When in the testing compartment birds were visually isolated from the rest of the group but remained in auditory contact. The testing compartment could be further subdivided into three smaller, adjoining compartments (Figure 19). Subjects were always trained and tested in the middle of these compartments (106 x 170 x 250cm), and during testing a group mate (referred to as the 'partner') was present in either one of the side compartments (297 x 170 x 250cm). Mesh windows (55 x 23 cm) were present in the dividing walls between the middle and side compartments so that birds had visual access to one another, and these windows could be removed during training to allow birds to walk in between the compartments. The experimenter stood in front of the middle of these compartments to bait and operate the apparatus throughout training and testing sessions.

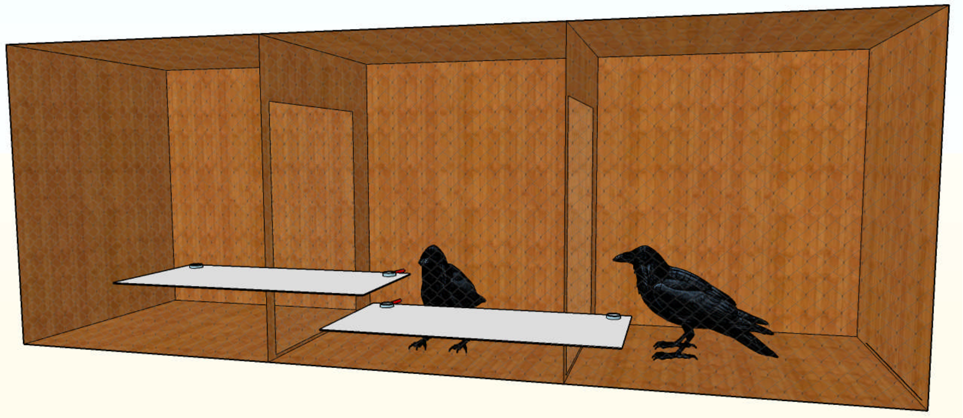

Figure 19. Test setup with subject in middle compartment and partner in one of the side compartments. Opaque trays the subject could choose to pull illustrated.

The apparatus consisted of two opaque, sliding trays, each of which could be temporarily mounted on one of two vertically aligned Perspex shelves that were affixed to the outer front of the testing compartments. Each tray spanned from the centre of the middle (subject's) compartment to one of the side compartments, and both trays vertically overlapped by 10cm in front of the middle compartment such that during trials subjects were given a choice between an upper and a lower tray (see Figure 19 for example). The trays were designed in this vertical manner to remove a confound associated with horizontally aligned trays, that prosocial choices may simply reflect a desire to be physically close to the social partner and to pull the nearest available tray from their preferred location. Each tray featured small cups fixed to each end to deliver food to middle and side compartments.

At the beginning of a trial, the trays were pushed forward so that the rope attached to the front of each tray was within reach by the subject. Subjects made a choice by pulling one of these ropes to slide the tray into reach of their compartment (and consequently one of the side compartments). Once the subject pulled one of the ropes, the experimenter pulled back the alternative tray so that the rope was no longer within reach. Importantly, the trays could also be switched between trials so that the tray that delivered a reward to the left or right compartment could be randomized between upper and lower shelves within a testing session.

Training

Prior to beginning testing, each subject completed a series of training steps to familiarize them with the apparatus and ensure that they understood the consequences of their choices. Given the cognitive demands of the apparatus, demonstration of understanding the apparatus was considered a vital prerequisite for starting test trials (see Tan *et al.* 2015 and Marshall-Pescini *et al.* 2016 for discussions). Subjects were always trained in the middle compartment. Training took place between May 2014 and January of 2015.

Step 1: In the first training step both trays were baited in the 1/0 position (1/0 denotes payoffs to subject and partner compartments, respectively), such that choosing either the upper or lower tray provided a reward to the subject (see Figure 20a). This step allowed birds to learn to pull the string and also allowed for any potential tray biases to be measured. Birds completed one session of 20 trials pulling either tray before moving on to Step 2.

Step 2: One tray was baited in the 1/0 position while the other was baited in the 0/0 position, so that birds needed to pay attention to where the food was placed before pulling (see Figure 20b). Criterion was set at a minimum of 15/20 trials correct (i.e., pulling the tray with the food on it) in each of two consecutive sessions, with the trays in a different position (i.e., the upper tray delivered to the left compartment and the lower tray to the right compartment, or vice versa) for each session. Subjects completed this step within 2-6 sessions (median: 3 sessions, or 60 trials).

Step 3: Both of the mesh windows were removed so that the subject could travel freely between the three compartments, and the trays were baited only on the outer sides (0/1; see Figure 20c). This step allowed subjects to learn that food rewards were delivered to the adjacent compartments, and again allowed for the measurement of any potential biases for the upper or lower tray. When beginning this step the birds had to initially be cued by the experimenter to the location of the food after pulling the string. Subjects met criterion after completing two consecutive sessions of 20 trials (40 trials total) pulling either tray to retrieve the food in the other compartments without any cuing from the experimenter. Once a bird met criterion in the session, in the following session the position of the trays was switched, so that, for example, in session 1 the upper tray delivered to the left compartment while in session 2 the lower tray delivered to the left compartment. Subjects completed Step 3 within 2-8 sessions (median: 4 sessions, or 80 trials).

Step 4: This final step ensured that subjects were attending to where each tray delivered food. Both trays were baited in the 0/1 position (delivering food to only the outside compartments) and the mesh window to one of the side compartments was closed while the other remained open (see Figure 20d). The position of the opening was alternated across sessions. In addition, the position of the trays was pseudo-randomized throughout each session so that for half of the 20 trials the lower tray delivered to the accessible compartment. There were no more than 4 consecutive trials of any tray position, to reduce the likelihood that subjects would learn any association or preference for one tray throughout the session. In order to complete the fourth training step and proceed to testing, subjects needed to choose the correct (delivering food to the accessible compartment) tray a minimum of 15 trials within a session, for two consecutive sessions. Subjects completed Step 4 within 5-35 sessions (median: 9.5, or 190 trials).

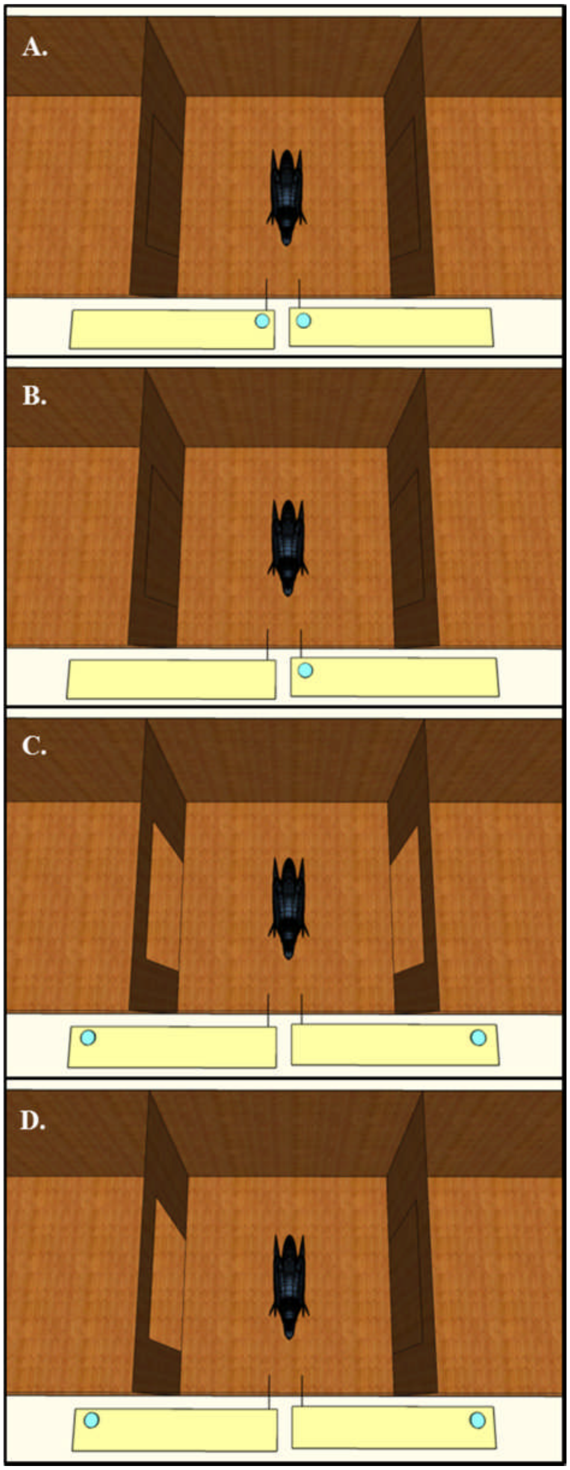

Figure 20. Top down view of training steps 1-4, described below. Distribution of food rewards is denoted with blue circles. Windows between compartments were made of wire mesh, but are depicted here as wood panels to more clearly distinguish between open and closed windows. Trays are vertically aligned in the centre of the subject's compartment, but are depicted laterally here for clarity. A) Step 1; B) Step 2; C) Step 3; D) Step 4.

Testing

Conditions

Each subject was tested in three conditions: 1) an affiliative condition, 2) a non-affiliative condition and 3) a non-social control condition (NSC), where no partner was present. Subjects received two sessions, each containing 20 trials, in each condition, with the position of the partner (left or right compartment) counterbalanced within dyads and between sessions. The order of sessions was: NSC, Dyad 1, Dyad 2, Dyad 2, Dyad 1, NSC. Dyad 1 was pseudorandomized across subjects as to whether the partner was an affiliate or non-affiliate partner (see Table 14). The relative payoffs for subjects and partners were the same in each test condition, such that subjects never received a reward for pulling on a test trial, but partners received one eighth a piece of Frolic©, a preferred food, if the tray corresponding to their compartment was pulled.

Test trials

Test sessions took place between September 2014 and April 2015, and were conducted in the mornings from 08:30-11:00 before the regularly scheduled feeding time. This was done to ensure that the birds were motivated to enter the testing compartment. Trials began when the trays were pushed forward so that the ropes were within reach, and lasted until the subject made a choice or until 45 seconds had elapsed. A choice was counted when the subject pulled the tray so that it moved; if the subject touched the strings without moving the tray this was not counted as a choice.

Each test trial had three possible outcomes:

Prosocial- Subject pulls the tray that delivers food to the recipient's compartment.

Asocial – Subject pulls the tray that delivers food to the empty compartment.

No pull – Subject does not pull either tray within 45s.

In order to ensure that birds were motivated to pull the trays, test trials were interspersed with motivation trials in which both of the trays were baited as 1/0, so that subjects could choose either tray to retrieve a reward for themselves only. Each testing session included 5 motivation trials: two at the beginning and subsequently one after every five test trials.

Behavioural data

For each test session, the behaviour of the subject and the partner, and the subject's choices (including those in the non-social control condition) were coded in the Observer XT Version 10 (see Table 15 for a list of all behaviour). A random selection of 20% of 34 (N = 7) sessions was independently re-coded by a research assistant uninvolved in the study and blind to the affiliation between subject and partner. A reliability score for each test session (all behaviours combined) was calculated using Observer XT, and these scores were then averaged across sessions to obtain an overall reliability score. Interobserver reliability was near excellent (mean Cohen's kappa = 0.79), indicating the videos had been coded reliably.

Table 15. Ethogram of subject and partner behaviours coded throughout test sessions and used as independent variables in the analyses

Category	**Behaviour**	**Definition**
Subject behaviour	Subject vocalize	Subject vocalizes whilst in sight. Vocalizations are considered one discrete response until bird has stopped vocalizing for at least 5s, in which case a new bout begins.
	Subject display	Subject erects feathers and assumes posture consistent with self-aggrandizing display. May be accompanied by vocalizations (described in (Boeckle *et al.* 2012)).
	Subject at partner window	Subject stands directly in front of window separating subject/partner compartments, facing window.
Partner behaviour	Partner vocalize	Partner vocalizes while in sight. Vocalizations are considered one discrete response until bird has stopped vocalizing for at least 5s, in which case a new bout begins.
	Partner display	Partner erects feathers and assumes posture consistent with self-aggrandizing display. May be accompanied by vocalizations (Boeckle *et al.* 2012).
	Partner directed attention-getting behaviour	Partner performs either of two behaviours: (i) Interact with tray: partner contacts either of the experimental shelves in front of their compartment with the beak (e.g., pecking or biting). (ii) Peck window: Partner pecks at mesh window separating subject/partner compartments. Usually this occurs as just one quick peck, but if they are pecking

		rapidly in succession this is considered one discrete event as well until there is a pause of two seconds between pecks.

Analyses

All data were analysed in IBM SPSS Statistics version 21, with the significance level set at $p < 0.05$. First, two-tailed non-parametric tests were employed on repeated measures data (e.g., Wilcoxon signed ranks test) using either a corrected prosocial tendency measure (discussed below) or proportional data to explore if as a group, the subjects' choices varied between conditions. Given the small sample sizes, exact p-values are reported (Mundry & Fischer 1998). Choice data at the level of each individual bird was then examined using chi-square goodness of fit tests to compare the proportion of no-pull responses across the three conditions, and binomial tests were used to examine prosocial choices within affiliate and non-affiliate conditions, with each individual's expected proportion of prosocial choices calculated by the number of times the subject delivered food to the corresponding compartment in the non-social control condition. Binomial tests were additionally used to measure individual biases for a particular tray (chance = 0.5; data presented in Table 17). Two subjects, LO and AD, failed to complete their last non-social control session due to lack of motivation and breeding respectively, therefore only their first three sessions (one non-social control, affiliate and nonaffiliate test session) were used in non-parametric analyses.

After analysing the raw data across conditions, Generalized Linear Mixed Models (GLMMs) were then used to examine the relative influence of various factors on test performance. GLMMs 1 and 2 examine whether session number or performance during training (specifically, the number of trials to meet criterion in the final training step 4) predicted performance on the test trials. GLMM 3 examines the influence of factors relating to the subject-partner relationship on corrected prosocial tendency values and GLMMs 4 and 5 measure how the subject and partner's behaviour predicted subject choices on a trial-by-trial basis. For all GLMMs, the full model is reported (Whittingham *et al.* 2006; Burnam & Anderson 2014).

GLMMs 1& 2: Session number and trials to criterion

To determine whether subjects' performance on the test trials was influenced by how quickly they demonstrated understanding of the apparatus in the training or experience over time, I ran two separate, binomial GLMMs with logit link functions using session number and trials to criterion (for training Step 4 only) as fixed factors, and subject and partner identity as random factors for both models. Dependent variables were number of trials in each session that subjects chose not to pull (GLMM1) and the number of prosocial choices in each session (GLMM2). For GLMM 1, four of the six subjects therefore had 6 data points entered into the model (one for each session), while LO and AD had 5 data points each (N = 34 data points total). For GLMM 2, each subject had 4 data points entered into the model (N = 24 data points total).

GLMM3: Corrected prosocial tendency (CPT) and subject-partner relationship variables

To correct for potential side preferences, a prosocial tendency score was calculated for each testing session. This was calculated in two steps: (i) the subject's preference for delivering food to the partner's compartment in each social session was subtracted from their preference for delivering food to the same compartment in the non-social control conditions: (Prosocial pulls for partner's compartment in test/total pulls in test)-(number of pulls for same compartment in control/total pulls in control). (ii) Depending on how large the subject's initial preference for delivering food to a particular compartment was in the non-social control they may have had more or less space to increase or decrease this preference in test trials, so a corrected prosocial tendency was calculated using the formula Pt'=Pt/Deviation Space (cf. Massen *et al.* 2011). Deviation space was calculated depending on whether the prosocial tendency was positive (DevSpace=1-side preference in NSC), or negative (DevSpace= side preference in NSC). These calculations provided each subject with one corrected prosocial tendency score per dyad session, and two prosocial tendencies per partner (one for when the partner is on the left, the other for when the partner is on the right).

The rank difference between subject and partner (-4–9), the relative sex of the partner (same sex vs. opposite sex) and the affiliation between the partner and the subject (affiliate, non-affiliate) were entered into the model as fixed factors, with CPT as the dependent variable. The CPT for each session was entered as one data point (N = 24 from 6 individuals) and subject and partner were entered as random factors to control for multiple sampling of individuals. As the data for CPT were normally distributed (Kolmogorov–Smirnov test for normality = 0.135, $p = 0.200$), GLMM3 was run using a normal distribution with an identity link function.

GLMMs 4&5: Subject/partner behaviour and subject choices

The aim of GLMMs 4 and 5 was to investigate, on a trial-by-trial basis, the influence of the subject's and partner's behaviour on whether or not the subject chose to pull (GLMM4, dependent variable: 'pull' (yes/no)) and when they did pull, whether they chose prosocially or asocially (GLMM5, dependent variable: 'choice'; all no-pull trials excluded). Each trial, rather than session, was entered as a data point in both models (N = 479 for GLMM 4 and N = 293 for GLMM 5) with subject identity, partner identity and session number entered as random factors to control for multiple sampling at these different levels. The same fixed factors were used for both models: subject display, subject at partner window, subject vocalize, partner vocalize, partner display, and partner directed attention-getting behaviour. Partner displays were analysed separately from partner attention-getting behaviour as the former may, in some contexts, be considered agonistic (Braun & Bugnyar 2012) and consequently have a differing influence on the subject's choices. All fixed factors were formatted as binary data to determine whether subjects' choices in each trial could be predicted by whether or not partners or subjects performed certain behaviours during the time immediately before subjects made a choice (the time period from choosing in the last trial until the next choice).

Results

Pulling vs. not pulling

Rather than continuing to pull at random throughout the sessions, most of the birds ceased pulling on 14 to 74% of test trials (median: 32%), while continuing to pull on 87-100% (median: 97%) of the motivation trials that were interspersed throughout the session. The rate of pulling on test trials decreased significantly over sessions ($F_{5,27} = 4.055$, $p = 0.007$), and was not predicted by the number of trials to criterion in the pre-training ($F_{1,27}$ = 1.210, coefficient = 0.003 ± 0.003, p = 0.281, r = 0.20). The random effects subject ID (Z = 1.290, p = 0.197) and partner ID (Z = 1.447, p = 0.148) were not significant. There was no significant difference in the proportion of pulls when a partner was present or not present (control sessions vs. test sessions grouped; Wilcoxon signed ranks test: N = 6, Z = -0.105, p = 0.938, r = 0.03), or between control, affiliate and non-affiliate conditions (Friedman's ANOVA: N = 6, χ^2 = 0.095, p = 0.994, Figure 21). Individual chi-square goodness of fit tests comparing rates of pulling across all three conditions revealed that one subject pulled significantly more in the non-social control condition than in affiliate and non-affiliate conditions (NO: χ^2 = 14.103, p < 0.001), while another subject pulled significantly less in the affiliate condition than in the non-affiliate and non-social control conditions (JO: χ^2 = 14.535, p < 0.001). A third individual pulled significantly more in the affiliate condition than in the non-affiliate and non-social control conditions (RY: χ^2 = 6.450, p = 0.040). For the remaining three subjects there was no significant difference in pulling across conditions (Table 16).

Table 16. Pulls across the three conditions. Results from individual chi-square goodness of fit tests comparing number of pull trials across non-social control (NSC), affiliate (Affil) and non-affiliate (NA) conditions. Significant results are italicized.

Subject	**NSC**	**Affil**	**NA**	χ^2	**P value**
NO	*32*	*17*	*9*	*14.103*	*P < 0.001*
GE	24	28	25	0.338	P = 0.843
JO	*37*	*12*	*37*	*14.535*	*P < 0.001*
AD	15	14	20	1.265	P = 0.530
RO	*7*	*17*	*7*	*6.450*	*P = 0.040*
LO	16	20	10	3.304	P = 0.192

Table 17. Table depicting the number of sessions for each subject to meet criterion (N = 20 trials per session), individual tray biases during all test trials assessed through binomial test with chance level of 0.5, and performance in each test session (prosocial pulls/all pulls). Non-social control sessions 1 and 6 depict number of pull trials only (maximum = 20). *, p < 0.01, **, p < 0.001.

ID	**Criterion**	**Tray Bias**	**Session Number**					
			1	**2**	**3**	**4**	**5**	**6**
NO	9	Upper**	20	10/16	4/6	1/3	0/1	13
GE	5	None	18	11/20	7/16	4/12	1/5	6
JO	10	Lower**	17	4/17	5/11	0/1	8/20	20
AD	5	Upper**	15	10/14	12/20	11/20	5/16	
RY	24	Upper*	5	3/5	2/6	6/11	0/2	2
LO	35	Upper**	16	5/20	6/10	9/20	11/20	

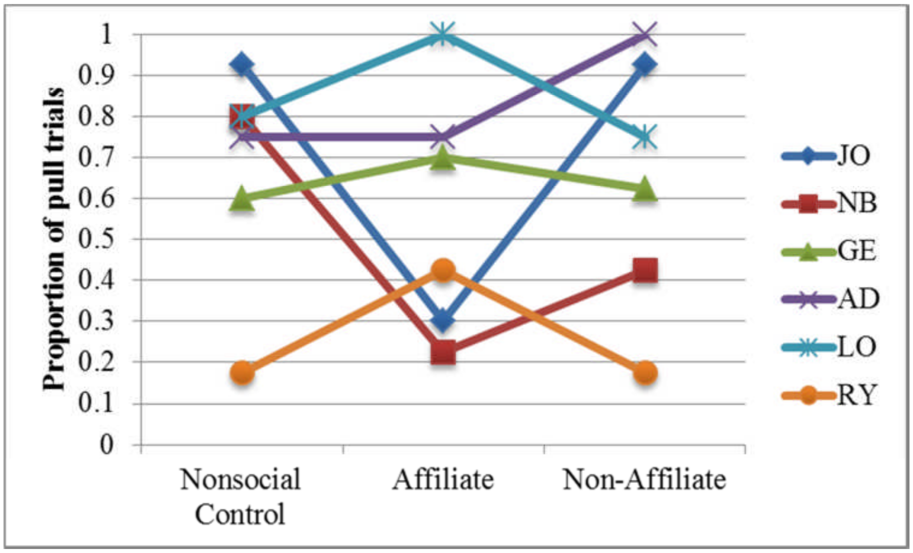

Figure 21. Individual data showing the proportion of trials in each condition (non-social control, affiliate and non-affiliate) where subjects chose to pull.

Prosocial pulls

Overall, when subjects did pull, there was no significant difference in the proportion of prosocial pulls toward affiliates or non-affiliates ($Z = -0.734$, N = 6, $p = 0.563$, $r = 0.21$; Figure 22) and similarly no significant difference between affiliate and non-affiliate conditions when corrected prosocial tendency was used as the dependent variable (Z = -1.363, N = 6, p = 0.219, r = 0.39). On an individual level, none of the subjects demonstrated any significant prosocial tendencies in either the affiliate or non-affiliate conditions (individual binomial tests, $p > 0.132$; Table 18). Instead, when pulling 5 of 6 subjects showed significant preferences for one tray, with four individuals preferring the upper tray and one individual preferring the lower tray. The rate of prosocial pulls did not change over session ($F_{3,19}$ = 2.206, p = 0.121) and was not predicted by performance in the pre-training ($F_{1,19}$ = 0.205, coefficient = -0.001 $\pm$ 0.001, p = 0.656, r = 0.10). Additionally, the random effects subject ID (Z = 0.968, p = 0.333) and partner ID (Z = 0.936, p = 0.349) were not significant. Each subjects' prosocial pulls, and number of pull trials per session is listed in Table 17.

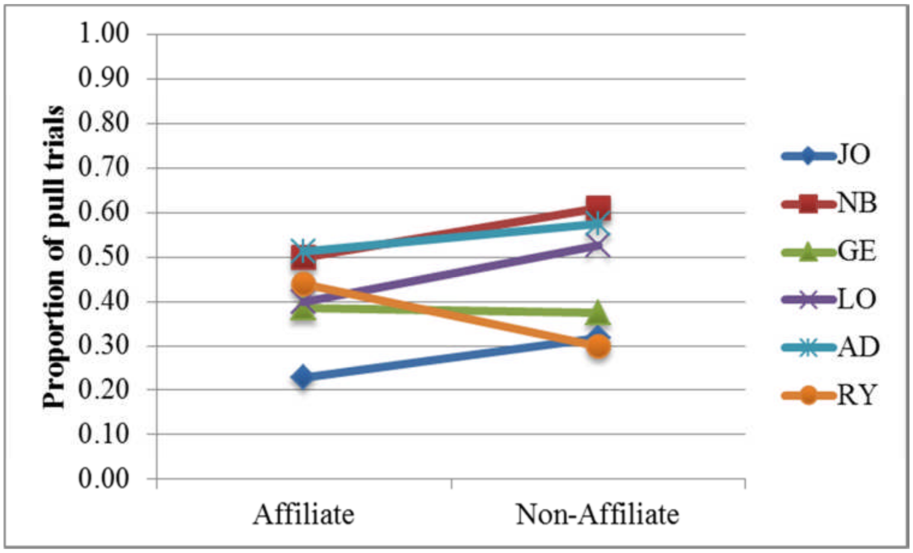

Figure 22. Individual data showing proportion of pull trials in affiliate or non-affiliate conditions when subjects pulled prosocially (pulled the tray that delivered to the partner's compartment).

Table 18. Results of individual binomial tests on total number of prosocial pulls, with chance level set as number of pulls delivered to the same compartment in control condition.

Subject	Expected proportion	Observed proportion	
		Affiliate	**Non Affiliate**
NB	0.31	0.56; *P*=0.223	0.27; *P*=0.962
GE	0.42	0.39; *P*=0.929	0.48; *P*=0.679
JO	0.46	0.42; *P*=0.998	0.32; *P*=0.133
AD	0.53	0.50; *P*=0.881	0.58; *P*=0.683
RY	0.43	0.47; *P*=0.917	0.43; *P*=1.000
LO	0.44	0.40; *P*=0.731	0.50; *P*=0.629

Behavioural data and partner identity

GLMM3: Corrected prosocial tendency and subject-partner relationship variables

To determine whether the subject's prosocial tendency was influenced by various aspects characterising the relationship between the subject and the partner, a GLMM with corrected prosocial tendency (CPT) as the dependent variable was run. Relative sex of the partner ($F_{1,20} = 0.662$, coefficient = 0.134 ± 0.165, $p = 0.425$, $r = 0.18$), affiliation ($F_{1,20} = 3.600$, coefficient = -0.286 ± 0.151, $p = 0.072$, $r = 0.40$) and relative rank of the partner ($F_{1,20} = 0.135$, coefficient = -0.008 ± 0.021, $p = 0.717$, $r = 0.08$), did not significantly predict subjects' overall prosocial tendency. The estimated variance of the random effect of partner was zero, and the remaining random effect of subject ($Z = 1.062$, $p = 0.288$) was not significant.

GLMM4: Pulling and partner/subject behaviour

In order to determine whether the behaviour of the subject or partner had any effect on whether or not the subject inhibited pulling on a trial-by-trial basis, a binomial GLMM with the binary dependent variable of pull or no pull was run. Attention-getting behaviour by the partner and social displays by the subject (see Table 13 for full description of behaviour) significantly predicted whether or not the subject pulled or not within a trial. Specifically, subjects were more likely to pull immediately after they displayed (Figure 23), and immediately following directed attention-getting behaviour by the partner such as pecking at the tray or the window (Figure 24). Displays by the partner, vocalizations by the subjects or partners and whether or not the subject spent time at the window to the partner's compartment had no significant effect on whether or not subjects pulled (Table 19). The random effects subject (Z = 1.141, *p* = 0.254), partner (Z = 1.271, *p* = 0.204) and session number (Z = 0.650, *p* = 0.516) were not significant.

Table 19. Full model assessed with binomial generalized linear mixed model (GLMM) with logit link function (N = 479 data points). Dependent variable was pull or no pull and subject, partner and session were entered as random factors. Test statistics (significant results in bold) and coefficients using 'pull' as the reference category ± standard error are shown.

	F value	**df1**	**df2**	**Coefficient**	**p-value**	**R**
Partner directed attention getting behaviour	3.976	1	472	0.665± 0.333	**0.047**	**.09**
Partner display	0.838	1	472	-0.407± 0.445	0.361	.04
Partner vocalize	0.169	1	472	0.143±0.348	0.827	.02
Subject display	4.146	1	472	1.694± 0.832	**0.042**	**.09**
Subject at partner window	0.333	1	472	-0.153± 0.265	0.564	.03
Subject vocalize	0.284	1	472	0.257±0.482	0. 594	.02

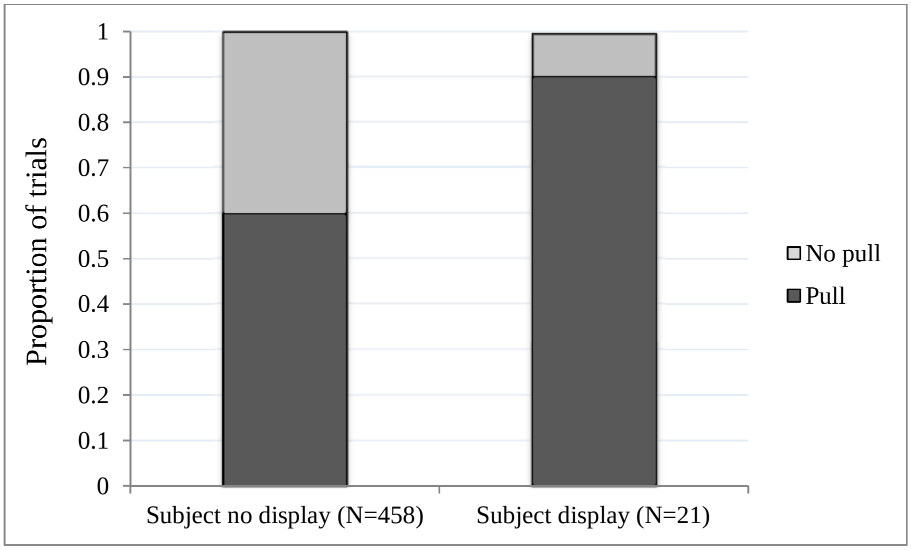

Figure 23. Proportion of trials in which subjects pulled the tray or did not pull the tray after displaying or not displaying.

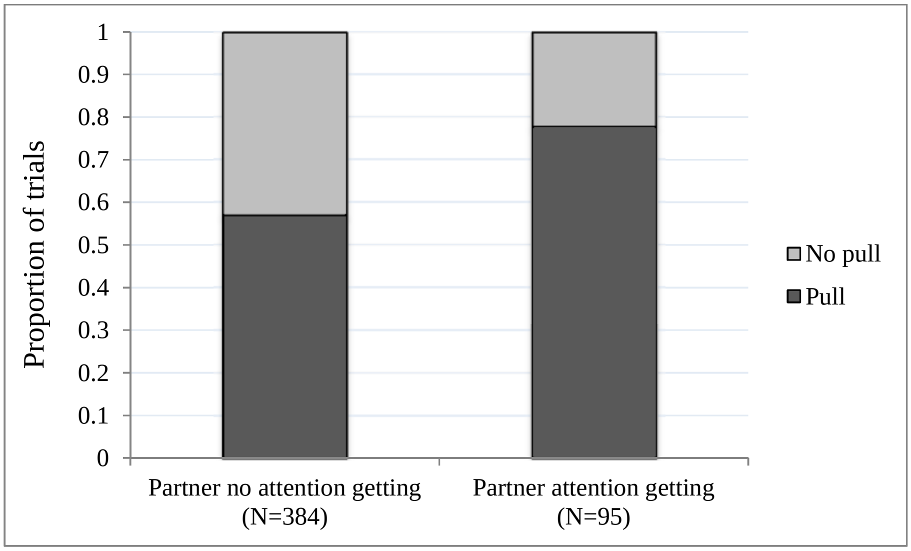

Figure 24. Proportion of trials in which subjects pulled the tray or did not pull the tray after attention getting, or no attention getting behaviour from the partner.

GLMM5: Prosocial vs. asocial choices and partner/subject behaviour

In order to determine whether the behaviour of the subject or partner had any effect on whether or not the subject chose prosocially on a trial-by-trial basis, a binomial GLMM with the binary dependent variable of prosocial or asocial pull was run. Displays and vocalizations by the partner or subject, attention getting behaviour by the partner and whether the subject was at the partner window immediately before pulling had no significant influence on whether or not the subject chose prosocially (Table 20). The estimated variance for both partner and session was zero, and the remaining random effect of subject ID (Z= 0.556, *p* = 0.578), was not significant.

Table 20. Results of GLMM 5. Full model assessed with generalized linear mixed model (GLMM) with binomial logit link function (N=293 data points). Dependent variable was prosocial or asocial pull and subject, partner and session were entered as random factors. Test statistics and coefficients ± standard error are shown.

	F	**df1**	**df2**	**Coefficient**	**p-value**	***R***
Partner directed attention getting behaviour	0.029	1	286	0.048 ± 0.282	0.866	.01
Partner vocalize	0.497	1	286	-0.231 ± 0.327	0.481	.04
Partner display	0.001	1	286	-0.013 ± 0.428	0.976	.00
Subject display	1.510	1	286	0.624 ± 0.507	0.220	.07

Subject at partner window	1.153	1	286	-0.294 ± 0.274	0.284	.06
Subject vocalize	0.026	1	286	-0.052 ± 0.324	0.872	.01

Discussion

Despite meeting strict pre-training criterion and demonstrating clear understanding of the apparatus, none of the birds demonstrated significantly prosocial or asocial tendencies when paired with affiliates or non-affiliates. These results are similar to those of chimpanzees, where subjects showed no difference in choices between control and partner conditions (Silk *et al.* 2005; Jensen *et al.* 2006; Vonk *et al.* 2008), or between different partner types such as kin or non-kin, dominants or subordinates (Silk *et al.* 2005; Jensen *et al.* 2006; Vonk *et al.* 2008; but see Horner *et al.* 2011). Factors related to the subject's relationship with the partner, including relative rank difference, affiliation and sex did not influence subjects' choices in either direction, again suggesting that the birds did not act with any regard to the identity or presence of their partner in the neighbouring compartment. While alternative explanations have been offered for the negative results of some of these studies (e.g., a lack of understanding, or attentional demands of visible food rewards) the revised methodology of the present study allows many of these alternatives to be ruled out so that the most likely conclusion is that subjects were not prosocial in this task. These results contribute to a growing body of evidence that corvids, and ravens in particular, consistently do not choose to benefit a conspecific if there is no direct benefit to themselves (Schwab *et al.* 2012; Di Lascio *et al.* 2013; Massen *et al.* 2015a).

In addition to pulling prosocially or asocially, the birds in this study could also choose not to pull on test trials; which indeed was expected if the birds were indifferent to the gains of their partners, as subjects were never rewarded on test trials. Instead of continuing to pull at random throughout the sessions, most of the birds did cease to pull on test trials when they received nothing for themselves, but continued to pull on the motivation trials that were interspersed throughout the session. Rather than occurring evenly across sessions, this lack of pulling increased with experience. At the group level, there was no difference in pulling between affiliates and non-affiliates. Similarly, the chimpanzees in Jensen *et al.*'s (2006) study did not pull when they received no rewards for themselves, but continued to pull on knowledge probe trials when they could retrieve the food delivered to the neighbouring compartment.

On a trial-by-trial basis, subjects performed socio-agonistic displays significantly more before pulling versus not pulling, and subjects' choices to pull were also significantly predicted by whether or not the partner performed any behaviours that would attract the attention of the subjects (i.e., pecking at the window between partner and subject compartments or interacting with the reward tray). The former finding is surprising as it could be predicted that subjects would choose not to act after performing a status show-off toward the partner. In other corvid species (e.g., rooks), food offering may serve a costly signalling function to convey information about the quality of the donor, with more dominant individuals transferring significantly more food items to conspecifics (Scheid *et al.* 2008). This may be one possibility for the increased number of pulls following dominance displays by the subjects in this study, however if this were the case it would be expected that subjects would choose prosocially, rather than at chance, after displaying. An alternative explanation is that displays corresponded with a heightened level of arousal and thus a greater likelihood of interacting with objects in the subject's immediate environment, similar to the displays of chimpanzees (Goodall 1964). Future studies could explicitly test this possibility by examining other markers of arousal (e.g., general activity level) and whether these vary systematically with displays.

Subjects pulled more just after partners performed attention getting behaviours, which may have aroused the subject or drawn their general attention to the trays. However, neither the behaviour of the partner nor the subject predicted prosocial or asocial choices. This suggests that rather than demonstrating needs or goals to the subject, the partner's behaviour may have incited an increase in general arousal that prompted the subject to pull a tray, but without specifically aiming to reward the partner. Such results should be taken into consideration when interpreting one-choice tasks such as the group service paradigm, in which subjects are only provided with one lever to pull in order to provision food to group-mates, and pulling rate is then compared to a control condition in which group-mates do not have access to the food delivered by the subject's pull. Consequently, pulling in the test condition results in only one (prosocial) outcome, in contrast to the prosocial or asocial choices afforded to subjects in this study. In the test condition when multiple partners are present and directing their attention to rewards subjects may be incited to pull significantly more than in control conditions, regardless of what the desired outcome is.

This study introduces several methodological changes that allowed for a more stringent assessment of prosocial tendencies. In particular, the apparatus was modified so that the position of the reward trays could be randomized throughout trials. Subjects had to first meet criterion with a strict, multi-step training scheme in which the tray position was frequently switched, so that they had to constantly attend to where each tray delivered rewards and therefore were unlikely to develop biases for one particular tray within a session. This same randomized scheme was used in testing sessions so that if subjects were other-regarding they had to constantly attend to the position of their trays and alter their choice of the upper or lower tray within a session to deliver rewards to their partner. Although the majority of birds developed preferences for a particular tray when pulling (see Table 17), this may not necessarily reflect any lack of understanding on the part of the birds, as subjects received equal rewards for pulling either tray (i.e., no rewards on test trials and one reward on motivation trials), and consequently there is no cost or benefit to switching tray preferences unless the birds are motivated to provision conspecifics. These continued biases for one option may serve as a useful heuristic to avoid having to make a deliberate choice on every trial (Ravignani *et al.* 2015). Instead, switching the trays throughout trials prevents any biased responding from resulting in a significantly prosocial preference. In addition, studies using two compartments typically reward subjects for delivering food to the neighbouring compartment during pre-training, which may result in these same preferences persisting throughout testing sessions when a partner is present (Tan *et al.* 2015). I used three compartments and ensured birds had equal experience of being rewarded for pulling and retrieving rewards from both prosocial and non-social compartments. Additionally, the trays were modified so that they were vertically aligned in the centre of the subject’s compartment, thus controlling for the possibility that subjects might choose a prosocial option because they prefer to be located or feed near conspecifics and simply pulled the tray closest to their preferred location, rather than being prosocially motivated.

It could be argued that the dynamic nature of the tray and partner positions may have made the tests overly complex and thus difficult for the birds to understand. For example, birds met criterion on the final training step after a median of 190 trials. It is possible that in such a large number of trials birds may have learnt a local contingency rule that enabled them to pass the training step, without fully understanding the apparatus. If this was the case, it would be expected that test performance would potentially differ for individuals who required more trials to pass training and may have not fully understood the apparatus. These results do not, however, support this idea, as individuals' performance in the test trials could not be explained by how quickly they met the pre-training criterion. Unfortunately it is difficult to assess how training performance compares to other tasks or other species as many studies either do not require subjects to meet criterion for knowledge of task contingencies (reviewed in Tan *et al.* 2015; Marshall-Pescini *et al.* 2016) or do not report the number of trials that subjects needed to reach this criterion (Burkart *et al.* 2007; Cronin *et al.* 2010; Mustoe *et al.* 2015). Those that have included this information are additionally difficult to compare as they require the subjects to attend to different features of the task such as the location of food or the quality of the food. For example, the subjects in Cronin *et al.* (2009) were required to reliably choose the baited tray among two vertical trays (each tray could be baited on either the donor's side or the recipient's side) and to retrieve the food from the location to which it was delivered. In this case subjects needed a median of 70 trials to meet criterion. This is most similar to training steps 2 and 3, in which subjects were required to attend to which tray held the reward (Step 2) and retrieve the food from the location corresponding to the tray pulled (Step 3; median of 60-80 trials to criterion for both steps). In a similar paradigm using different reward distributions, capuchin monkeys required a median of 100 trials in order to reliably choose a tray with two high-value rewards over a tray with one high value and one low value reward (Lakshminarayanan & Santos 2008). In the current setup the ravens were required to constantly reassess which of the equally-baited trays delivered food to the accessible compartment, the location of which additionally varied across sessions. Given the rigorous nature of this training scheme it might be expected that subjects would require more trials to reach criterion. In addition to including such pre-tests in future studies (Tan *et al.* 2015; Marshall-Pescini *et al.* 2016), I suggest that providing data on the number of trials or sessions to reach this criterion will allow for between-species and between-task comparisons that will aid in designing future paradigms.

One of the primary limitations of this study is the small sample size. These results need further replication with a larger number of individuals, while continuing to examine prosocial preferences on an individual level. Despite this small sample size, none of the subjects showed any tendency to choose prosocially at an individual level. It could be argued that.by testing birds in the morning before feeding, increased hunger could have created a more competitive context which would reduce the likelihood of food provisioning; however subjects also received food rewards throughout the test session (during motivation trials, which are described below). Additionally, as a routine food cacher (Bugnyar *et al.* 2007), ravens frequently have access to food items outside of their normal feeding times. These results are consistent with previous studies that have found no evidence for prosociality in captive ravens using different methods, including token exchange (Massen *et al.* 2015a) and allowing conspecifics to access food rewards (Di Lascio *et al.* 2013). Although this study found no effect of recipient identity on prosocial tendencies, a potentially interesting avenue for future research would be to examine factors related to the subject's identity; for example by testing whether more socially integrated individuals (determined using social network analysis) are more likely to behave prosocially toward conspecifics. Unfortunately as all birds in this study performed at chance levels for prosocial or asocial choices, this was not possible to test due to the lack of variation in test scores. It is also notable that some of the final testing sessions overlapped with the beginning of the breeding season, however analyses showed no effect of session number (or order) on either pulls or prosocial choices. Taken together these results provide convergent evidence that ravens do not preferentially act to benefit conspecifics, and consequently the range of cooperative behaviours they exhibit in the wild may not be guided by prosocial motivations *per se*.

Notably, this study was performed with mainly sub-adult birds that had not yet formed the species-typical monogamous pair bonds which have been predicted to show the strongest expression of prosociality in other species (Cronin 2012), and may not yet have fully developed their social cognitive abilities. The social world of a subadult raven is arguably more complex than that of an adult pair-bonded bird as during this time the birds form large aggregations that also consist of smaller, socialized subgroups (Braun *et al.* 2012). It is during this period that the birds must keep track of complex dominance hierarchies and form their own affiliate relationships. Sub-adult ravens are already capable of understanding third-party relationships among conspecifics (Massen *et al.* 2014b) and additionally, the birds in this study have already shown that they attend to the relative efforts and payoffs of cooperative partners (Massen *et al.* 2015b), and thus it would be expected that a similar level of understanding would operate in the present study. In order for prosocial tendencies to emerge in this task however, prosocial motivation, in additional to social cognitive skill, is needed. It thus appears that the ravens' performance in this task may be attributed to a lack of prosocial motivation in this particular context.

In sum, this study introduced several methodological changes that may benefit future tests of prosocial preferences, including a rigorous counterbalancing scheme, strict pre-training criterion for understanding the task and interspersed motivation trials showing that failure to pull was not explicable by a general learned irrelevance. The results from this revised paradigm show that when given the option to benefit conspecifics at a small cost to themselves, ravens do not choose to do so, regardless of conspecific identity or behaviour – a result that thus far appears consistent in this species across several different paradigms, suggesting that ravens may indeed have earned their collective name, an 'unkindness'.

Chapter 7. General Discussion

Summary of findings

In the wild, animals are faced with a plethora of information from their environment, and must learn to selectively attend to and use the most relevant of this information in order to survive and reproduce (summarized in Table 21; Shettleworth 1998). In the physical domain, the key challenges faced by animals have to do with locating and obtaining food. Tool use is one such method that has allowed animals from a range of different species to exploit new ecological niches (e.g., the New Caledonian crow’s tool use allows it to fill the niche of the woodpecker; Hunt 1996). In environments with a greater degree of variation (in terms of season, resource availability, etc.), individuals would further benefit from cognitive mechanisms that allow them to respond flexibly to a range of problems (e.g., instead of relying only on sticks as probing tools, understanding that any rigid object can be used; Niemala *et al.* 2013). Although it has frequently been theorized that unrewarded object exploration may be a useful avenue for coming to learn about the functional properties of objects, this has rarely been explicitly tested in nonhuman animals (Power 2000). Additionally, it is unknown whether unrewarded object exploration can be goal directed, in order to explicitly seek information about an object’s functionality. The research presented in this thesis provides preliminary evidence that unrewarded object exploration allows birds to form and test predictions about the way that an object behaves, which can then be applied toward solving novel problems, but found no evidence that birds strategically change their behaviour to learn about an object’s functionality.

In the social domain, access to resources and mating opportunities is often dictated by an individual’s relationship with other group members, in terms of social ranking or sexual bonds (Byrne & Whiten 1989). Affiliative relationships in particular are characterized by prosocial behaviours such as grooming/preening and agonistic support, but whether the actors performs this behaviour out of some regard for their partner’s welfare (as humans generally do) is a topic of debate (Silk *et al.* 2005; Silk 2007; Vonk *et al.* 2008; Cronin *et al.* 2010; House *et al.* 2012). Additionally, most of the studies in this field have focused on primates, and consequently less is known about the psychological underpinnings of prosocial behaviour in other species, and what factors may promote prosocial behaviour. The research presented in Chapter 6 suggests that subadult ravens, which frequently show prosocial behaviour in the wild, are not psychologically motivated to behave prosocially toward group members, and that prosocial choices are not influenced by the behaviour or identity of the potential recipient.

Table 21. Challenges faced by birds in the wild, in either the physical or social domain. The 'current understanding' column details what we currently know about how animals respond to these challenges in nature, and the 'knowledge gaps' column describes aspects of cognition relating to these challenges that are poorly understood. The 'results' column details how the research in this thesis has addressed these knowledge gaps.

	Physical Environment	**Social Environment**
Challenges faced in the wild	• Navigating the environment • Obtaining food	• Competition for access to mates and resources
Current understanding	• Repeated interaction with objects in the physical environment affords learning opportunities (Power 2000) • A few birds species use external objects as tools to access otherwise unobtainable food (Shumaker *et al.* 2011) • Many species which use tools are also those that frequently explore objects (Power 2000)	• Access to these resources can be determined by affiliative relationships, or strong bonds between individuals (Byrne & Whiten 1989) • These bonds are characterized by prosocial behaviours between individuals (e.g., agonistic support or preening; Silk & House 2011)
Knowledge gaps	• Do birds learn about objects through exploration? • Do birds explore objects strategically to gain information?	• Do prosocial behaviours reflect a psychological predisposition to benefit the welfare of others? • Are these prosocial behaviours influenced by the identity or behaviour of the recipient?
How this thesis addresses	• Systematically examines the role of exploration in learning about object	• Examines whether birds show prosocial preferences, and what

knowledge gaps	affordances	factors influence these preferences
Results	• Birds form and test predictions about the way that objects behave through exploration. • Information learnt during exploration can then be applied to solve new problems.	• Birds do not show unsolicited prosocial preferences toward group members, including close social partners. • Prosocial choices are not influenced by the behaviour or identity of the recipient.

Chapter 4a: Tool use by greater vasa parrots

The observational data presented in Chapter 4 documents the occurrence of habitual tool use among a captive population of greater vasa parrots, a species which until now was not known to use tools. All of the birds in this study (N = 10) interacted with seashells that were present on their aviary floor, and which had been introduced as a source of calcium for the birds, by picking the shells up in the beak and using the lower mandible to bite off small pieces which were then swallowed. Half (N = 5) of the individuals in the group also used small pebbles, or the pits of dates leftover from feedings, to scrape against the inside of these shells, resulting in smaller particles of shell which were then licked off of the tool or ingested directly. This grinding behaviour is unusual in the animal kingdom; whereas a number of species use stick tools to access out of reach food, or stone tools to break open encased food, no reports thus far have documented an animal using a tool to actually process its food (e.g., by grinding). Furthermore, these tools were transferred between conspecifics on numerous occasions; a behaviour which has thus far only been documented among chimpanzees (Pruetz & Lindshield 2012).

In addition to the novelty of the behaviour, another interesting aspect of the vasa parrot’s tool use is that incidents of tool use (and general interactions with the seashells) were concentrated around a period just prior to the breeding season, which in birds, results in an increased need for calcium to produce eggs (Brenninkmeijer *et al.* 1997; Pahl *et al.* 1997). This would suggest an interesting role for tool use in the vasa parrot’s reproduction, but first needs to be confirmed with further data on whether tools are regularly used exclusively before breeding. Most of the birds employed more than one type of object as tools on the seashells, although these were categorically similar (both date pits and pebbles are small, round and hard). This raises the question of whether the birds chose the objects they used as tools based on an understanding of the properties that make a good grinding tool. As discussed in Chapter 2, one of the key ingredients for this more creative tool use is a propensity to explore external objects, which may either give individuals experience with different physical properties or provide the raw behavioural sequences which may later be incorporated into tool use. Vasa parrots are an ideal species for testing this assumption as they frequently manipulate objects in captivity. The experimental data presented in Chapter 4 addressed this question by investigating what features of novel objects vasa parrots attend to.

Chapter 4b: Novel object exploration by greater vasa parrots

The experimental portion of Chapter 4 demonstrates that when encountering novel objects, vasa parrots perform a range of exploratory behaviours toward these objects. Depending on the object, these behaviours can generally be divided into general exploratory behaviours, such as contacting with the beak, or "relevant" behaviours such as picking up with the beak, which provide information about the hidden, structural properties of the objects. Taken together, these exploratory behaviours (and particularly the relevant behaviours) allow the birds to gain some general idea of how that object behaves. When later encountering similar objects that differ only in visual properties (i.e., colour), there was no significant difference in the duration or quality of exploration that birds direct toward these objects relative to the baseline object they were presented with, suggesting that the vasa's exploration is not driven by visual novelty alone. However, when encountering objects that violate expectations concerning how an object should behave (e.g., a rope which is suddenly rigid instead of flexible), vasa parrots spend a significantly greater proportion of their exploration time engaged in behaviours which provide them with structural information. These data suggest that the birds are trying to gain information about the objects' properties as they interact with them. Rather than changing their behaviour immediately upon first encountering the structural properties of the objects, however, this change in investigative behaviour seemed to take place more gradually over the course of the trial.

The vasa's performance is consistent with that of another explorative parrot species, the kakariki, which also increases and qualitatively changes its exploration when presented with objects which look familiar, but behave differently (Demery 2013). Although these findings need to be confirmed in other psittacines, they support the general idea that exploration allows parrots (and potentially other species) to form general predictions about their environment. This is also similar to the behaviour of human infants, who change both the duration and quality of their haptic manipulation when encountering structurally novel objects (Steele & Pederson 1977; Ruff *et al.* 1984; Streri & Spelke 1988; Streri *et al.* 2000; Streri 2003). In contrast, the performance of the vasas differs from that of chimpanzees, which when presented with objects that are visually novel, will increase their attention toward these objects, but will not do so when presented with visually familiar objects that are structurally different. A key difference between these two studies that may contribute to this pattern of results is the context in which the objects were presented; whereas the vasas were allowed to freely explore the objects in their home aviary, the chimpanzees were required to manipulate the objects to obtain a food reward (Povinelli & Dunphy-Lelii 2001).

Broadly speaking, the results of this chapter suggest that object exploration does provide individuals with information about the structural properties of objects, and that individuals will qualitatively target their exploration towards learning more about these structural properties if they violate previous expectations of how that object should behave. These results raise two key questions, however: i) can the information learned during exploration then be applied toward solving a problem and ii) can exploration be used strategically? These questions were addressed in Chapter 5.

Chapter 5: Function and flexibility of object exploration in kea and New Caledonian crows

The experiment presented in Chapter 5 aimed at explicitly testing i) whether any information encoded during exploration can be retrieved by the individual in a problem-solving context, and ii) whether individuals change the duration or quality of their exploration in order to learn about functionally relevant object properties, once they have encountered a specific task requiring a certain type of tool. The results of this chapter show marked differences in exploratory behaviour between kea and New Caledonian crows, with kea spending a significantly greater proportion of time exploring the objects. When then allowed to use the information acquired during exploring toward solving a task, several birds from each species performed significantly above chance, primarily when the colour of the objects was associated with functionality as opposed to pattern. Crucially, these individuals then performed at chance levels when tested with objects that they were not allowed to explore beforehand (despite also featuring colour as a visual cue associated with functionality). Similarly, a group-level analysis showed that performance across all subjects was significantly higher in an exploration condition relative to a non-exploration condition. This indicates that valuable information about object properties is obtained during exploration which can then be recalled and used to aid problem-solving. This finding, however, should be interpreted with caution, as one individual performed above chance in the control condition despite having no experience with the objects, illustrating that other strategies which may not require understanding of object properties could have been used by birds who performed well in the exploration conditions. Additionally, despite the general facilitatory role of exploration in problem-solving, the precise aspects of exploration (quality or duration) which facilitate learning remain unknown, as there was no significant relationship between test performance and the quantity or quality of exploration.

For both the kea and crows, there was no significant difference in the amount of time that they spent exploring the novel objects before or after having learned that the objects have a functional relevance. This was evident not only in overall duration of exploration, but in the type of behaviours used to explore the objects, such that birds did not perform more behaviour which would provide information about the functional properties of the objects after having encountered the problem solving task. This result suggests that individuals do not actively seek information about the functional properties of objects.

Chapter 6: Prosocial behaviour in captive ravens

The data on tool transfer in Chapter 4 and tool sharing in other primate populations anecdotally suggests that other animals behave prosocially toward one another, although the motivation or cognitive mechanisms underlying this prosociality are unknown. Chapter 6 shifts away from problem-solving in the physical domain to investigate how birds operate within their social environments, and, more specifically, whether they will act to benefit conspecifics at little or no cost to themselves. Using a revised paradigm which addresses several weaknesses that have been highlighted in previous studies of animal prosociality, the data from Chapter 6 suggest that despite demonstrating an understanding of the experimental setup, captive ravens do not act to benefit conspecifics in the absence of self-gain; rather, individuals generally stopped pulling trays which delivered food to neighbouring compartments on trials in which they received nothing for themselves.

Additionally, individuals did not choose any differently for birds with whom they were closely affiliated compared to birds with which they did not have a particularly close relationship. At a behavioural level, arousal seemed to play some role in subjects' choices, as subjects were more likely to pull just after performing displays. Additionally, whether or not a subject pulled was predicted by whether or not the partner had just performed a behaviour which would draw the attention of the subject either to the trays or to the partner's compartment. Although both of these factors influenced pulling behaviour, they did not influence *which* tray the subjects chose. These results are most similar to studies of chimpanzees, in which subjects generally ceased to pull in the absence of rewards for themselves, and did not change their pulling or prosocial preferences depending on the identity of their partner (Silk *et al.* 2005; Jensen *et al.* 2006; Vonk *et al.* 2008; but see Horner *et al.* 2011). These results suggest that sub-adult ravens do not act to intentionally benefit conspecifics, and, taken together with other recent studies, suggest that corvids (and ravens in particular) are not prosocial.

Synthesis of results

A review of the existing literature shows that despite its presence across several taxa, tool-using behaviour is incredibly rare, and even more so when considering cases of habitual tool use where several members of a population use tools on more than one occasion (Shumaker *et al.* 2011). Within the order Psittaciformes, only two species have been documented habitually using tools outside of an experimental context, with black palm cockatoos using nuts for social displays and hyacinth macaws using leaves as wedges to position nuts in their beak. One proposed explanation for the general rarity of tool use in the animal kingdom is that there are “few ecological contexts in which tools are superior to the already evolved anatomy of the animal” (Hansell & Ruxton 2008, p76). The curved beak of a parrot is not well-adapted for manipulating objects such as stick tools, but is well adapted for extractive foraging given its sheer strength and unique bill tip organ which is located on its end (Hansell & Ruxton 2008; Demery *et al.* 2011). This, coupled with the parrot’s grasping, zygodactyl feet, may leave little necessity for the use of external objects in foraging or other contexts.

Nonetheless, when taken together with other recent reports of spontaneous tool use in captive parrots (Auersperg *et al.* 2010; Auersperg *et al.* 2012), these data suggest that a range of parrot species have, at the very least the capacity for tool use. Rather than serving as evidence of absence, the absence of data on tool-using behaviour in wild birds is more likely to do with the general lack of data on wild parrot behaviour and the difficulty of carrying out long-term observations on these birds, which generally inhabit the upper layers of forest canopies. It may be that with an increased focus on parrot behaviour in general, additional reports of tool use in other species will emerge, as they have with primates and cetaceans (Goodall 1964; Beck 1976; Krützen *et al.* 2005).

Species that live in dynamic environments must attend to and learn about range of changing properties within these environments, such as the location of ephemeral food sources (Shettleworth 1998). These changing environments would favour individuals that are able to extract relevant information and flexibly apply this information in novel contexts (Niemelä *et al.* 2013). In the case of tool use, individuals may benefit from such cognitive flexibility by selecting tools based on their functional properties rather than through a lengthy trial and error learning process (Call 2012), but how animals initially come to learn about these properties, or about specific objects in their surroundings, is not well understood. The current literature on object exploration in nonhuman animals suggests that exploring and manipulating objects in the external environment confers several advantages in terms of learning about the physical world (summarized in Power 2000). This is supported by data showing that tool-using species are generally more exploratory than non-tool-using species, but very little research has focused on what properties of the objects are actually being attended to during exploration. The data on vasa parrots presented in this thesis strengthen the link between tool use and object exploration by documenting tool use in a highly explorative parrot species and further demonstrating that these birds attend to the underlying structure of objects as they explore them. It is important to note, however, that a similar attention to structural novelty has been documented in non-tool-using kakarikis (Demery 2013). Taken together these results broadly suggest that novel object exploration allows animals to form and test hypotheses about the world, and while this may be particularly advantageous for tool use, it is not unique to tool-using species. This may not necessarily mean, however, that the individuals possess some representation of how this object might function in different contexts, or that they could then apply this information that had been learned in the absence of direct reinforcement toward solving a novel problem.

This last possibility - that nonhuman animals gain relevant information from exploring objects which can be later applied to solve problems - is a fact that has widely been taken for granted in current studies of physical cognition. To date, a limited number of studies have included “built-in” exploration phases in which subjects are required to interact with potential tools, and later choose among these to solve a task (Povinelli 2000; Manrique *et al.* 2010; Manrique *et al.* 2011; Povinelli & Ballew 2012). Some of these studies suggest that exploration does indeed provide critical experience which can be applied to solve problems; however they also neglect a key question, which is how these abilities function in a natural context (Manrique *et al.* 2010; Manrique *et al.* 2011). Chapter 5 provides tentative evidence that after exploring objects outside of a problem-solving context, individuals can indeed apply information gained during this exploration to later choose objects which may function as tools. Furthermore, despite the implied role of exploration in problem-solving, until now it was virtually unknown whether animals can use this behaviour strategically to acquire relevant information to solve a task (but see Visalberghi *et al.* 2009 for an exception). Chapter 5 suggests that when allowed to interact freely with novel objects, both tool-using and non-tool-using species do not change their exploration strategies in order to acquire information from objects that would facilitate problem solving.

When considered together, the empirical data from Chapters 4 and 5 ultimately show that object exploration provides individuals with information about physical properties, including hidden structural properties such as weight and rigidity. During exploration individuals seem to form predictions about how objects are likely to behave, and respond to changes in these structural properties in order to refine these predictions (similar to Demery 2013, and also discussed in Chappell *et al.* 2012). This ability to selectively attend to and learn about different object properties may be especially beneficial in the wild for animals such as parrots, which typically occupy large ranges within tropical forests and rely on a more general, omnivorous diet in contrast to highly specialist foragers (e.g., some raptor species hunt primarily one prey type; Terraube *et al.* 2011). In these cases frequent exploration and behavioural flexibility may allow them to discover novel food sources or means of accessing otherwise unobtainable food (e.g. encased food; Borsari & Ottoni 2005). There is further evidence that the information gained during exploration may then be abstracted in order to use objects in a functional way, but that structural properties are more easily generalized to objects with salient visual features such as colour. Intriguingly, although individuals may change their exploratory tactics in response to structural novelty it does not appear that this is done intentionally, as it is not used in a strategic fashion to seek functional information about which objects could potentially work as tools. This may represent a metacognitive challenge as individuals are potentially required to make judgments about their own knowledge (e.g., or lack of) in order to seek this information. A recent review found strong evidence for this type of information seeking in primates, but inconclusive evidence from other species including dogs, rats and pigeons, although this requires further study (Roberts *et al.* 2012). Additionally, the birds would have needed to anticipate that they would be allowed access to the baited apparatus following exploration, which may have posed an additional cognitive challenge associated with planning for the future (Suddendorf & Corballis 2007).

Turning to avian social cognition, the data from Chapter 6 show that ravens will not intentionally provision conspecifics at little or no cost to themselves. This is in line with data from a range of primate species as well as several other studies of corvids using different paradigms (Silk *et al.* 2005; Schwab *et al.* 2012; Di Lascio *et al.* 2013; Massen *et al.* 2015a). Corvids have been highlighted for studies of prosociality due to their social complexity and remarkable performance on other social cognitive tasks, which suggest that they are able to recognize individuals, track relationships among them and adjust their behaviour based on predictions of how these individuals might behave (e.g., re-caching food if a conspecific was watching; Dally *et al.* 2005; Bugnyar 2011; Massen *et al.* 2014b, Bugnyar *et al.* 2016). Corvids (and also many primate species) also show a range of cooperative behaviours in the wild; they engage in joint territory defence, will support partners during and after agonistic encounters and cooperate to rear and provision their young (Heinrich 2007; Fraser & Bugnyar 2010, 2012; Massen *et al.* 2014a). Additionally, food sharing occurs between close social partners during development, but when tested using this task (von Bayern *et al.* 2007; Scheid *et al.* 2008), these same close social partners did not choose to provision one another. One striking, anecdotal example of this was when two closely-affiliated birds entered the testing compartment and prior to the start of the testing session, the subject shared food with his partner. In the task this bird then showed no obvious prosocial tendencies. This is similar to the performance of jackdaws, which show quite extreme levels of food sharing during ontogeny by providing food to a range of potential social partners, but jackdaws are nonetheless not prosocial in a food sharing task (von Bayern *et al.* 2007; Schwab *et al.* 2012).

In general, food sharing is a rare behaviour in nature outside of parent-offspring dyads which is often hormonally driven (e.g., meerkat helpers with higher cortisol levels provision pups more; Carlson *et al.* 2006; Soares *et al.* 2010) and primarily occurs in reaction to begging, theft or harassment (Jaeggi & Van Schaik 2011). Given the rarity of food sharing in the wild, we may need to rethink our current reliance on using food donation as a means to measure prosocial motivations across species, particularly as food is an especially salient stimulus for animals and desire to retrieve it may override executive function mechanisms. This relates to a broader tension within the field of comparative cognition between presenting numerous species with identical tasks (MacLean *et al.* 2012) in order to make accurate inferences about differences in cognitive ability, and using tasks which are 'fair' to the species being studied and more closely mirror their socio-ecology and behaviour in the wild (Shettleworth 1998). In the case of prosociality, it may be fruitful and informative to further examine the prosocial preferences of different species using paradigms that more closely mirror their behaviour in the wild. One possibility for object-focused species such as vasas or kea would be to determine whether individuals will provide conspecifics with access to desired objects, even if they themselves are not allowed to access them.

In summary, this thesis has used several new and modified approaches to test how birds navigate their dynamic physical and social environments, with Chapters 4 and 5 systematically focusing on the role of exploration in learning about object properties, and Chapter 6 using a revised and more rigorous methodology to examine prosocial preferences in ravens. These approaches therefore provide important new data on aspects of avian cognition that are little understood, and in doing so raise a number of new questions and suggest exciting new avenues for future research, which are discussed below.

Directions for future research

A large part of this thesis has focused on the behaviour and cognitive abilities of parrots, which are frequently cited for their sophisticated problem-solving skills. In actuality, very little is known about parrot behaviour and cognition. Instead, most of our assumptions about parrots' mental capabilities are derived from data revealing the relatively large brain size of parrots, as well as the performance of only one or two individuals from one or two species. Alex the African grey parrot is a prime example of this, as until very recently many of our conclusions about the intelligence of parrots were fuelled by studies highlighting the performance of this one individual (Emery 2006; Emery & Clayton 2009; Pepperberg 2009). There are over 350 parrot species on 5 different continents which occupy vastly different ecological niches and show marked variation in sociality, and although new research is beginning to improve our understanding of these birds (e.g., Liedtke *et al.* 2010; Demery 2013; Krasheninnikova 2014), the cognition of the vast majority of species remains unstudied. Similar to the approach taken with corvids in which a range of different species have been studied which allows for more general conclusions to be made regarding their cognitive abilities, more empirical work is needed on a range of different parrot species using larger sample sizes in order to fully understand what these birds are using their big brains for, and how variations in these abilities might be explained in terms of environment.

By extension, even less is known about parrot behaviour in the wild (e.g., only one published study exists on greater vasa parrot behaviour in the wild, focusing on breeding; Ekstrom *et al.* 2007). This may be due in part to the challenges of conducting research on a taxon which typically inhabits dense forests and is able to travel large distances within minutes (Gilardi & Munn 1998). Nevertheless, studies of wild parrots are valuable for understanding the validity of research carried out in captivity; particularly as recent research suggests that captive and wild individuals may show differences in problem-solving ability (Benson-Amram *et al.* 2013). For example, data comparing the innovative tendencies of captive and wild animals have found that captive animals show lower levels of neophobia and higher levels of exploratory behaviour due to their experience with manmade objects and captive settings, and that these behaviours predict how likely they are to innovate solutions to novel problems (Benson-Amram *et al.* 2013; Haslam 2013). One particularly striking example is that of the silver fox, which when bred over dozens of generations for 'tameness', or reduced fear of humans, showed several marked changes in sociocognitive performance as a correlated by-product, particularly when dealing with tasks involving manmade materials (Hare *et al.* 2005; Trut *et al.* 2009). Regarding the present research, field observations are needed to assess whether vasa parrots use tools and/or frequently explore objects in the wild, or whether these behaviours are restricted to either one population or to captive settings generally. In a similar vein, captive kea showed greater levels of exploration than New Caledonian crows, but whether a similar difference would be found with wild kea is - although highly likely - unknown.

The data on tool use in vasa parrots also raise questions about the development, function and cognitive drivers of this behaviour. Functionally, it may be that the use of a tool i) increases foraging efficiency by allowing individuals to acquire smaller, more easily ingested pieces (including particles in the case of grinding) from the shell which cannot easily be bitten off from the beak alone, or ii) that it mitigates discomfort from scraping the beak against the surface of the shell. Although it was not possible to conduct further experiments with the captive population tested in Chapter 4, these possibilities could be tested by presenting birds with seashells covered in substances of varying degrees of difficulty to scrape off (e.g., smeared on fig paste versus baked on fig paste) to determine whether some birds preferentially use tools to obtain substances that are difficult to access with the beak alone, or whether they use tools in all instances to avoid scraping the beak on the shell. Another possibility is that the tools may compensate for limitations imposed by beak morphology (e.g., the smaller, curvier shells may be difficult to fit the lower beak into) which could be tested by presenting birds with shells of differing size (large versus small) and shape (curvy versus flat) to determine whether birds preferentially use tools on particular shell types.

Another related possibility, discussed at length in Chapter 4, is that the smaller pieces of shell obtained through tool use allow calcium from the shell to be retained more easily, and that this behaviour is concentrated prior to breeding when calcium requirements are especially high. Although tool-using birds were primarily male, these calcium benefits could be passed on to females through the regurgitative feeding common to this species during breeding season, and females may prefer calcium rich regurgitation. This type of courtship feeding could provide substantial fitness benefits to both males and females by contributing to egg production (Steele 1986; Gwynne 1988). For example, male-female pairs of gulls which engage in frequent courtship feeding tend to lay larger eggs than female-female pairs, which rarely engage in courtship feeding (Hunt 1980). Additionally, the rate of courtship feeding among gulls correlates with the demands of egg production, such that rate of feeding peaks around the time that the energy demands of eggs production peak (Helfenstein *et al.* 2003). These possibilities could be further tested through longitudinal data determining whether tool use occurs regularly prior to breeding, as well as through manipulating calcium levels in the diet to determine whether tool use occurs less frequently on a calcium rich diet. Observational studies on the relationship between copulation rate and tool-using rate could further test whether females prefer calcium rich crop regurgitation and thus whether ultimately males gain more copulations if they engage in this type of tool use.

In addition to the outstanding questions that concern the role that tool use might play in this species' biology, how this behaviour originated also requires further investigation. In the absence of longitudinal and developmental data, it is nearly impossible to determine how the behaviour began or spread throughout the group, although the extremely high levels of social tolerance among these birds would support a scenario in which it was learnt socially. Developmental studies providing groups of fledged birds with controlled access to the seashells either in the presence or absence of a tool-using adult would elucidate whether tool use reflects an innate predisposition or is socially learned.

Finally, as many of the vasas used more than one type of object on the tool, this raises the question of whether they were chosen based on visual (small and round) or functional (hard) properties. Whether birds chose the objects they used as tools based on these functional properties could be determined by allowing birds to select from a range of similar objects that vary in terms of their visible (size, shape) or hidden properties (e.g., identical objects that vary in hardness).

Developmental studies have identified exploration as a key process in how young infants and children gain knowledge about their environment and solve physical problems (Piaget 1952; Gibson 1988). It is therefore surprising that, given its accepted importance in human cognitive development, the role of exploration in how nonhuman animals learn about object properties and solve physical problems has thus far received little focus, and particularly when considering comparative data revealing a strong link between explorative tendency and tool use in primate and bird species. The data presented in Chapter 5 represent one of the first in-depth examinations of what animals learn from their exploration and whether they use exploration strategically. Additional research with other species is needed to confirm the results presented in Chapter 5, as well as to examine other potential benefits that exploration may confer in terms of motor skill or an increased rate of innovation. In addition to elucidating the function of exploration, the results of such studies could generate valuable insight into the type of experiences that form an animal's understanding of its physical environment, which in turn might account for differences between species.

Correlations between behavioural traits (including explorative tendency) and physical cognition could additionally be examined on an individual level. In each of the studies presented, there were noticeable differences between individuals in how they behaved and approached the task. This individual variation is an important source of material for natural selection to act on (Darwin 1859; Thornton & Lukas 2012), and given the small sample sizes that characterize studies of avian cognition, may be a particularly important factor to account for. Furthermore, studies have found that these stable individual traits predict how individuals within a species use external information and cope with environmental change (Herborn *et al.* 2014).

Further studies that include individual measures of traits such as neophobia, explorative tendency and inhibitory control may therefore provide important data on the key behavioural drivers of innovation and problem solving both within and between species.

It is important to note that each of these studies focuses on distinct species, and therefore while the results of this thesis allow us to make broad inferences about exploration and physical cognitive abilities in nonhuman animals, further research is needed to determine whether some of the differences in results between Chapters 4 and 5 are due to species differences. For example, it could be that the performance of the vasas in Chapter 4 represents an underlying cognitive difference between this species and the kea and crows, and they perhaps would have performed differently from the kea and New Caledonian crows when exploring objects with a task in mind. Unfortunately due to limitations at the study site this was not possible to test. A key strength of Chapters 4 and 5, however, is that they capitalize on the subjects' natural behavioural propensities (i.e., to explore objects). This approach could be further applied to studies of prosociality in other species, such that rather than testing prosocial preferences through food provisioning, future research could focus on prosociality in contexts that more closely resemble a species' behaviour in the wild.

Concluding remarks

To conclude, the research presented in this thesis examines how large-brained corvids and parrots use information within both their physical and social environments. Data are presented on a new form of tool use in a parrot species, as well as the potential role that object exploration plays in innovations such as tool use. These results provide preliminary evidence that birds may gain information about the novel structural properties of objects through unrewarded exploration. Such structural information may be associated with salient visual features of objects, allowing knowledge gained from exploration to facilitate problem solving, but individuals do not seem to strategically change their exploration with problem-solving tasks in mind. Within the social domain, corvids demonstrate competence in attending to multiple dynamic stimuli to retrieve food for themselves, but will not use this same information to provision conspecifics in the absence of self-gain. Parrots and corvids are therefore adept at learning and using different types of physical information to solve problems, but may not explicitly seek this information or use it to benefit others.

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