

Comparative cognition and behavioural flexibility in two species of neotropical parrots.

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**COMPARATIVE COGNITION AND BEHAVIOURAL
FLEXIBILITY IN TWO SPECIES OF NEOTROPICAL PARROTS**

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Thesis submitted in partial fulfilment of the requirements of the Degree of
Doctor of Philosophy

30 August 2013

Statement of originality

I, Jayden Owen van Horik, confirm that the research included within this thesis is my own work or that where it has been carried out in collaboration with, or supported by others, that this is duly acknowledged below and my contribution indicated. Previously published material is also acknowledged below.

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Details of collaboration

This thesis incorporates work carried out in collaboration with Dr. Alice Auersperg from the Department of Cognitive Biology, University of Vienna, Austria. The collaboration related to the methodological design of Chapter 3.2: Familiar Object Exploration for use in a comparative study involving numerous species of corvids and parrots. All data collection, analysis and subsequent interpretation of the results pertaining to this experiment, as included in this thesis, are however entirely my own.

The General Introduction is adapted from two published review articles that are noted in the following section on publications arising from this thesis. While this work was reviewed by the associated co-authors, I am the primary author of this work.

Publications arising from this thesis

Review articles

van Horik, J., Clayton, N. & Emery, N. (2012) Convergent evolution of cognition in corvids, apes and other animals. IN: Vonk, J., & Shackelford, T. (eds.) *Oxford Handbook of Comparative Evolutionary Psychology*. New York: Oxford University Press

van Horik, J. & Emery, N. (2011) Evolution of cognition. *WIREs: Cognitive Science*, 2, 621-633.

General Abstract

Similarities in brain size, life histories, psychology and behaviour in parrots, corvids and apes suggest that certain socio-ecological selection pressures may have driven the convergent evolution of cognition in these families. However, very little is known about parrot behaviour and cognition, outside of African greys and kea. Therefore, captive red-shouldered macaws (*Diopsittaca nobilis*) and black-headed caiques (*Pionites melanocephala*) were presented with a variety of tasks to assess their social and physical cognition and behavioural flexibility. Although these species possess many similarities in their life history and ecology, there are also substantial differences in their morphology and natural habitats that could have driven differences in their cognitive evolution. Observations of social and physical interactions in both species revealed that macaws engaged in high levels of affiliative behaviour, and object neophobia, whereas caiques displayed high levels of social play and object exploration. However, such differences did not appear to result in differences in their social or physical cognition. Macaws and caiques displayed comparable performances on Serial Reversal Learning tasks (as an index of behavioural flexibility). Both species also demonstrated similar performances on two Means-End transfer tasks and a series of innovative foraging tasks that were designed to assess their comprehension of object relationships. However, macaws and caiques appeared to solve such problems by generalising learned information across novel tasks. Overall, these findings suggest that these two species may approach certain socio-ecological problems using flexible cognition that may be generalised across different problems, supporting claims for a domain general intelligence.

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1.1: Thesis Overview

The central aim of this thesis is to investigate cognition in two species of Neotropical parrots, red-shouldered macaws (*Diopsittaca nobilis*) and black-headed caiques (*Pionites melanocephala*). These particular species possess a similar brain size, which is relatively large for their body mass, and comparable to other species of parrots, corvids and apes (Iwaniuk et al., 2005). Investigating behaviour and cognition in these species may therefore provide clues to the socio-ecological selection pressures that have been suggested to have lead to a convergence in cognitive evolution between apes and birds (Emery and Clayton, 2004a).

While the relative brain size of red-shouldered macaws and black-headed caiques are comparable, each species is characterised by contrasting aspects of their natural ecologies. Macaws inhabit open wooded environments whereas caiques inhabit closed canopy forest (Juniper and Parr, 2003). Consequently, each species may experience different environmental challenges. For example, caiques may experience a fluctuating availability of resources in a closed canopy environment, whereas macaws may experience a relatively more stable supply in an open habitat. Such ecological differences may then promote adaptive specialisations in their foraging behaviours, as selection pressures shape foraging efficiency with respect to each particular habitat (Glickman and Sroges, 1966, Mettke-Hofmann et al., 2002). Similarly, selection pressures may also promote differences in the social aspects of these species. Cognition has therefore been considered to have evolved in response to adaptive selection pressures that are associated within specific domains, particularly those associated with social and physical interactions with the surrounding environment (Shettleworth, 2010). However, domain specific intelligence, such as the capacity for tool use, may then be generalised across different domains through processes such as behavioural flexibility (Emery and Clayton, 2004a). Hence, selection pressures may promote cognitive adaptations that favour an understanding of the underlying functionality of tool use. Such

cognitive adaptations may then be transferred across the physical domain to aid in solving problems in the social domain, such as learning about how to manufacture or use tools through social observation.

The first chapter (**Chapter 1**) introduces the field of research on the evolution of cognition, with a particular focus on the cognitive divergences between humans and our closest living ancestors, the non-human great apes. This chapter then discusses current evidence in support of a convergent evolution of cognition between relatively large brained species of birds and mammals. A contemporary review of research on parrot cognition is also provided.

As little is known about red-shouldered macaws and black-headed caiques in captivity or in the wild, **Chapter 2** provides a baseline study on the social dynamics and behaviours of these species. Behavioural observations revealed substantial between-species differences. Macaws invest a greater amount of time in affiliative allopreening behaviours and are more social than caiques. Conversely, caiques were observed to participate in social play behaviours more than macaws. Dominance hierarchies and pair-bonded relationships were also quantified for subsequent reflections on individual behaviours.

The experiments in **Chapter 3** were conducted to investigate whether differences in the natural ecologies of these species correspond with differences in their propensities for object exploration. Macaws were highly neophobic and demonstrated relatively low levels of familiar object manipulation. Caiques by contrast showed low neophobia and interacted with a much greater variety and diversity of objects than macaws. The relationships between object exploration and the natural ecology of each species are discussed with respect to the demands of generalised or specialised foraging behaviours.

Chapter 4 investigates whether different propensities to interact with objects influence innovative foraging behaviours. In the wild, foraging innovations

tend to be impaired in species that are highly neophobic (Reader and Laland, 2003). Neophobic species may be less likely to approach novel objects or places and therefore unlikely to reveal the affordances of such interactions. Findings from this study reveal that macaws and caiques demonstrate similar capacities to solve a series of innovative foraging problems, irrespective of differences in their propensities to interact with objects. Macaws and caiques possess a comparable brain size, which has been demonstrated to correlate positively with rates of innovation (Lefebvre et al., 1997). Such findings therefore suggest that differences in neophobia may have little overall influence on foraging innovations. Alternative mechanisms that might drive variation in innovative rates are discussed in light of these findings.

To further investigate whether between-species differences in object exploration influence an understanding of object relationships, two means-end tasks were presented to subjects in **Chapter 5** to assess their capacities for physical cognition. Both species demonstrated comparable performances on a task requiring an ability to discriminate between the functional properties of connected and disrupted materials to retrieve a reward. While subjects rapidly solved a task using familiar materials, their performances were however impaired when presented with novel materials. In a second means-end task, a new Trap-Gaps paradigm, subjects were presented with a more challenging problem that required substantial experience to learn to discriminate between accessible and inaccessible foods based on size relationships. A transfer task was then designed to assess whether subjects required similar trial-and-error experience to relearn a functionally equivalent, but novel problem, or whether they could generalise learned information across tasks. One caique spontaneously solved the transfer task. These findings reveal that macaws and caiques demonstrate a comparable understanding of object relationships to corvids and primates, and suggest that their performances on such tasks may be mediated by higher-order cognitive mechanisms.

Macaws and caiques demonstrated flexibility in their behaviours on innovative foraging and means-end tasks. In **Chapter 6**, subjects were therefore presented with two serial reversal learning (SRL) tasks that have previously been considered an index of behavioural flexibility. Moreover, a comparative study of the performances of corvids on SRL tasks suggests that social complexity underlies such flexibility (Bond et al., 2007). While behavioural observations revealed that macaws were more social than caiques, both species demonstrated comparable performances on a SRL task involving colour discriminations. To further investigate the mechanisms underlying such flexibility, subjects were presented with a subsequent SRL task that varied the strength of the learned pre-reversal associations. Subjects trained to a highly reinforced pre-reversal criterion were faster to respond to the reversed contingencies than subjects in the low reinforcement condition. Macaws and caiques therefore used the highly reinforced associations to generate a conditional *win stay-lose shift* rule, rather than learning each new association by lower-level processes of conditioning and extinction. These findings suggest that higher-order cognitive mechanisms may facilitate behavioural flexibility in macaws and caiques.

Together, the experiments presented in these chapters reveal comparable performances of macaws and caiques on a series of tasks that assess physical and social cognition. Such abilities occur irrespective of observed differences in their social dynamics, their different propensities to interact with objects, and differences in their natural habitats. While cognition may have evolved in response to domain specific challenges, the cognitive capacities of these species are suggestive of a domain general intelligence. Hence, large brains may afford capacities for higher-order cognitive mechanisms to generalise information across different domains through processes of behavioural flexibility.

1.2: Evolution of Cognition

The way in which animals respond behaviourally to changes in their environment varies considerably, yet functions to maximise their fitness. In many species, responses occur at fundamental levels, such as reflexes, orienting, taxis, and simple forms of learning, such as habituation and sensitisation. However, some species respond using more sophisticated psychological processes, such as conditioning, memory, and reasoning, to predict and even manipulate environmental regularities. As such, cognition can be described as the ability to acquire, process, and retain information, which can then be used to influence decision making (Shettleworth, 2010). Such processes are commonly inferred when animals apply generalised principles obtained from learned experiences to solve novel problems. It is thus in the manipulation of 'knowing that' information (declarative; episodic and semantic), rather than 'knowing how' information (procedural), that animals may demonstrate reasoning about the underlying causality of problems they experience in their environment (Shettleworth, 2010).

Darwin (1897) noted that certain behaviours found in non-humans, such as imitation, tool use, and the use of sounds in communication may provide insights into human intellect. Consequently, he concluded 'the difference in mind between man and the higher animals, great as it is, certainly is one of degree and not of kind' (Darwin, 1897, p. 128). Although research in comparative psychology has progressed considerably since Darwin, similar key questions remain today as to whether animals, like humans, possess a number of cognitive abilities that collectively contribute to their intelligence (Premack, 2007, Wasserman, 1993). Research on animal intelligence has traditionally focused on our closest living relatives, the great apes, based on the erroneous view of a 'ladder of life' or 'scala naturae', which places humans at the top and apes, dolphins, birds, reptiles, fish, amphibians, and insects below in relative order (Hodos and Campbell, 1969). As a result, the special status of apes, based on their evolutionary relationship to humans, has predisposed views that cognition in non-human animals is largely focused

within the primate family. This elementary approach soon developed into a phylogenetic model based on the tree of life, maintaining similar assumptions that complex cognition (so-called intelligence) is coupled with recent evolutionary events (Healy et al., 2009).

However, cognitive evolution does not conform to a simple linear scale aligned with phylogeny. Irrespective of phylogenetic relationships, species may share commonalities in the socio-ecological challenges they face in their environments (Seed et al., 2009, Shettleworth, 2010). Such problems might include learning about the nutritional values of certain foods, the location, and timing of ephemeral resources, or the recognition of a territory, nesting or dwelling site relative to local landmarks. Common ecological selection pressures, like those responsible for analogous (i.e., convergent) evolution of flight in bats and birds, might then converge on similar cognitive functions due to how an organism interacts with its habitat rather than its ancestry (Emery and Clayton, 2004a). Thus, the comparison of cognitive processes among more distantly related species, such as birds and mammals and their particular environments, might also reveal clues to how cognition evolved (Lewontin, 1998).

METHODS FOR RECONSTRUCTING THE EVOLUTION OF COGNITION

To describe how cognitive traits may have evolved, changes in the history of observed characteristics of living and extinct ancestral species that may be proxies for behaviour and cognition need to be examined. Such tangible clues such as nest building, burrowing sites, or stone-tool artefacts may provide the best clues we have because behaviour does not fossilise. Aspects of cognitive evolution may be inferred by describing changes in the length and shape of certain bones, cranial size, and patterns in brain endocasts or fossil materials found with other fossil remains, but what is more important are those actions in extant species with clues to cognitive functioning, such as patterns of locomotion, manual dexterity, food gathering, and communal activities (Gould and Lewontin, 1979). Indeed, this is how biological

anthropologists reconstruct views of what human ancestral life may have been like. For example, we can observe the adaptation of bipedal locomotion from skeletal remains, leading to speculation about whether the hands were freed to carry objects or make tools, freeing the mouth and facilitating vocal communication. Did an increase in cranial size support the enlargement of the frontal and temporal lobes furthering linguistic capabilities? What about evidence for the cognitive processes underlying the use of fire, hunting with tools, religion, or the production of art? Are these mere speculations ('Just So Stories') that fit our assumptions or viable, testable hypotheses?

Phylogenetic Analyses

If we revisit Darwin's statement—the distinction between human and non-human intelligence is one of degree, not of kind—we might expect there to be no qualitative differences in cognition between species (Macphail and Barlow, 1985). That is, cognition is governed by general processes common to all animals. This claim has been supported by experimental psychologists who proclaim basic rules of association account for learning and memory throughout the animal kingdom (Macphail and Barlow, 1985). The General Process view considers that the fundamentals of complex cognition result from the strengthening of positive, neutral, or negative responses that are paired with associative stimuli and applied across an extensive range of problems (Papini, 2002). Although simpler processes, such as habituation, are shared by all species, there may also be qualitative between-species differences in capacities for conditioning, problem solving, and the formation of abstract concepts, which may be restricted to more cognitive species. Of the greatest complexity—said to be unique to humans, but with precursors in other animals—is language (Hauser et al., 2002). While we may differ only in degree from our closest non-human relatives, chimpanzees, which share about 98% of our genetic profile (Lewontin, 1998), major cognitive changes have occurred during human evolution. Humans and chimpanzees might be very similar in their DNA, but are vastly different in the size and structure of their brains and their resulting cognitive faculties (Sherwood et al., 2008).

Ecological Correlates of Cognition

It is possible, with the use of large data sets, to demonstrate global trends across species and infer relationships between cognitive traits and socio-ecological variables (Nunn and Barton, 2001). However, caution is warranted as methodological inconsistencies may confound interpretations. For example, experimental designs need to incorporate ecologically valid approaches, as it may be illogical to rank complex cognition among different species with different life histories (Bitterman, 1975, Chittka and Niven, 2009). Thus, behaviour may be influenced by a number of processes that are not specifically cognitive. For example, polygynous species may require a larger home range to successfully breed, whereas monogamous species, which have ready access to mates, may not. As a result, differences in species' ecologies may influence their spatial memory abilities. To control for such variation, alternative methods that incorporate more comparable cognitive correlates such as relative brain size may prove more productive.

Brain Size and Cognitive Ability

Larger organisms tend to possess larger brains than smaller organisms. However, overall brain size per se is not a particularly useful proxy for cognitive ability. This is because brains are composed of many components that are not directly associated with cognition, but serve to control sensory, visceral, and motor functions. For this reason, measures of cognitive capacity are often gauged by comparing those areas of the brain more closely associated with cognition, such as the neocortex in mammals and the nidopallium (cortex equivalent) in birds (Jarvis, et al., 2005), with an organism's overall body mass. The resulting measure is referred to as relative brain size.

Hypotheses about the function of relatively large brains have generally focused on the relationship between relative brain size and correlates of cognition such as behavioural innovation, group size, social learning, and tool

use (Healy and Rowe, 2007). This connection assumes that larger brains must be functionally adaptive considering the increased energetic costs associated with maintaining them (Striedter, 2005). Although studies on vertebrate species generally support this view, investigations into the cognitive mechanisms that underpin invertebrate behaviour contest whether bigger brains are actually better (Chittka and Niven, 2009). In mammals, primates and dolphins have the largest brains for their body weight, with humans showing the largest overall relative brain size (Roth and Dicke, 2005). Trends also appear for larger brains during vertebrate evolution (Striedter, 2005). As a result, birds, although generally considered inferior in intellect to mammals, have larger, more cortically based brains and are thus considered more intelligent than their evolutionary predecessors, the reptiles. Surprisingly, however, some birds such as parrots and corvids (crows, rooks, jays, etc.) possess brains that are relatively comparable in size to those of chimpanzees (Emery and Clayton, 2005). Recent research also suggests that parrots and corvids share many of the features believed to be associated with advanced cognitive processing in primates such as high sociality, longevity, slow development, long parental investment, as well as a large forebrain size (Emery and Clayton, 2004b).

A relatively large forebrain in birds is thought to be associated with innovative behaviour (Lefebvre et al., 2004). A large brain size may allow species to behave flexibly, enhance their ability to learn quickly, and thus adapt to environmental irregularities. Species that respond rapidly to novel or ephemeral food sources, or develop innovative foraging techniques, such as using tools, might benefit from accessing additional resources. Cognitive adaptations may subsequently influence species fitness by reducing extinction risk or enhancing invasion success (Sol et al., 2005).

In fact, brain size appears to be correlated with a number of ecological factors and life history traits throughout different taxonomic groups (Striedter, 2005). Although forebrain size in birds is particularly associated with innovative behaviour, brain size (neocortex) in primates and ungulates is more closely

linked to social dynamics, such as group size and intra-group coordination (Dunbar and Shultz, 2007).

Sociality has thus influenced complex social intelligence such as tactical deception and social learning (Fitch et al., 2010). However, bird sociality differs from primate sociality. Flock size in birds often varies seasonally and at times can comprise thousands if not millions of individuals. As such, sociality per se does not appear to correlate with brain size in birds; instead it may be the type and quality of bonded relationships that are more influential (Emery et al., 2007).

Interpretations of correlations may therefore be confounded by differences in species' life histories. Frugivorous primates tend to have larger brains and larger home ranges than foliovores. As such, a large home range size might be necessary to accommodate the spatial and temporal variations in fruit supply, whereas leaves that are abundant year-round permit smaller home ranges. Nonetheless, other species that share polygynous or promiscuous mating systems also exploit large home ranges (Harvey et al., 1980). Locating mates or tracking resources throughout large home ranges might require certain cognitive capacities that result in an advanced spatial memory or sophisticated mental maps. For example, spatial cognition of food-storing birds may appear to have driven an increase in brain size. However, evidence to support such claims remains controversial (Healy and Rowe, 2007). Such discrepancies provide clear examples that large home ranges are not necessarily good predictors of large brains. Furthermore, these studies emphasise the importance of focusing on specific brain components, such as the hippocampus (in the case of spatial memory and caching), rather than brain size per se.

Methodological Problems

Using large data sets to interpret correlations between brain size and behavioural traits has resulted in numerous hypotheses, but they should be

treated with some caution (Healy and Rowe, 2007). In an attempt to increase sample sizes, researchers have integrated data from a variety of studies, some with different intentions that use different methods. Brain size, for example, has been calculated using post-mortem and frozen tissue, structural neuro-imaging data, and brain sections processed using outdated methods. Proxies of brain size have also been derived from cranial volume (Striedter, 2005). Few studies attempt to address individual-specific factors such as age, which is known to influence brain size. Different measurements for body weight have also been applied, including substituting body weight for brain stem volume (Striedter, 2005). Thus the application of such a variety of controversial measurements may, as a result, obscure comparisons and compromise the integrity of interpretations, particularly if they are not consistent within a study. Large bodied species also tend to have large brains and may thus require larger neurons and hence more brain mass to process equivalent cognitive information compared to small-bodied organisms such as invertebrates (Chittka and Niven, 2009).

The use of collated data sets detailing incidences of complex cognition as represented by behavioural flexibility and innovation, initiated by Lefebvre and colleagues (2004), has been integral to the analysis of species-wide comparisons in brain size. However, the frequency of reported instances of such behaviours may be subject to inadvertent observer bias. For example, large, diurnal species distributed within close proximity to human settlements may be more frequently observed than small, nocturnal species that reside in inaccessible habitats. Experimental versus observational accounts of behaviour may also fall prone to reporter bias. Incidences of social learning, for example, may easily be inferred by field observations but more difficult to establish experimentally in the laboratory.

Caution is also required when defining analogous traits (i.e., those traits that arise independently among unrelated species through processes of convergent evolution), as ecological correlations between distantly related species are likely to be fundamentally different. Generalised definitions of

social bonds or group structures, for example, between birds and mammals may not be directly comparable or representative of different species' life histories. As such, assumptions that social complexity, for example, has arisen from increased group size may be an over-generalisation of more complex behaviour. Social organisation in ungulates or flock size in birds, for example, is dynamic and varies throughout both time and space. Indeed, there appears to be no relationship between flock size and brain size in birds (Emery et al., 2007), although birds that engage in complex forms of social cognition appear to have relatively large brains (Pravosudov and de Kort, 2006).

When inferring cognitive abilities as the result of environmental selection pressures, it is also important to consider the phylogenetic relatedness of species. Species may exhibit similar characteristics not because they share similar environments, but because they are closely related. Any cognitive similarities may therefore have been inherited from a common ancestor rather than having been evolved independently under similar selection pressures. By considering species as independent data points, irrespective of their phylogenetic relationships, analyses may overestimate the importance of any relationships between variables (Nunn and Barton, 2001), which dramatically enhance the probability of obtaining positive associations. It is therefore important to correct for phylogeny by using approaches such as independent contrasts (Felsenstein, 1985). Independent traits that then occur repetitively across species can be more confidently identified as adaptive.

Comparative Analyses

An alternative approach to the generalised mechanisms thought responsible for enhanced cognition is that cognition is adaptive and domain specific (Pinker, 2010). Such adaptations may arise to solve specific problems associated with particular environments and then be generalised and applied to novel situations. This hypothesis emphasises an ecological perspective, focusing on how an animal's environment shapes its cognitive abilities (Healy

et al., 2009, Shettleworth, 1993). Natural selection shapes the morphology and behaviour of organisms in terms of differential survival and reproduction. Consequently, distantly related species may converge on similar cognitive characteristics due to shared environmental selection pressures. Adaptive changes caused by natural selection may also lead species to converge on similarities such as omnivory, agility, or acute vision; characteristics required for success in certain habitats such as dense forest. Similarly, animals that occupy the vast open plains of Africa might share characteristics of an herbivorous lifestyle. To determine whether such selection pressures produce similar cognitive abilities across species, it is necessary to systematically compare differences and similarities in cognitive tasks between closely as well as distantly related species. As such, different species that inhabit similar environments may develop similar intellectual abilities, enabling them to better survive in specific habitats. Species may therefore differ not only in degree, but also in the nature of their intelligence.

Comparing Abilities

The comparison of closely related species with different ecologies is essential when investigating cognitive adaptations. Any divergence in cognitive ability may therefore be attributed to independent evolution under different selection pressures (Papini, 2002). Many corvids and parids, for example, store food for retrieval in periods of food scarcity. Within these two families, some species store more food than others and depending on the species and their environment, recovery can occur from hours to months later. Such differences in caching propensity and latency of retrieval may then result in species-specific differences in spatial memory. Thus by comparing memory among closely related species within the same family, ecological influences on certain cognitive and neural processes may be revealed. Although research in this area has provided mixed results, it has been proposed that birds that store more food have a better spatial memory than those that do not. Support for this hypothesis is from a positive correlation between the relative size (and thus 'storage' capacity) of the hippocampus, the brain area involved with

spatial memory processing, and the caching propensity of a given species.

Comparisons between distantly related species may also provide valuable insights into convergent evolution of cognition (Emery and Clayton, 2004a). Although any comparisons between distantly related species must account for differences in perceptual and/or morphological characteristics, similarities in life history traits and environmental conditions might provide analogous cues to the development of cognition. For example, the convergent evolution of complex cognition in apes and corvids is thought attributable to shared environmental pressures (Emery and Clayton, 2004a, Seed et al., 2009a). Such comparisons are supported by the fact that both groups are omnivorous, visual animals that live in complex social groups and demonstrate sophisticated forms of object manipulation, manifest in extractive foraging, and tool use.

When evaluating species differences, it is important that any assessments are ecologically representative of the challenges that individual species could confront in their environment. In this regard, standardised tests may not necessarily account for differences in a species' physical ability. It is thus important to adopt paradigms that can be generalised and applied to numerous species irrespective of their physical capabilities. For example, a battery of tests that incorporates functional similarities, but varies in terms of its independent variables, such as retention intervals or levels of difficulty, can allow direct comparisons of cognitive processes between distantly related species such as apes, dolphins, and birds. However, such tasks should not be too difficult that most animals fail, or too easy that they all pass, resulting in 'floor' or 'ceiling' results that obscure group differences. Potentially unavoidable experimental circumstances may also confound interpretations. For example, when comparing human children with chimpanzees, it is the children who are tested by members of their own species, probably while their mothers are present, whereas apes are tested by another species (humans) on a task designed by humans (Boesch, 2007).

Why an Evolutionary Approach is Important

By comparing differences in cognitive abilities across species, inferences can not only be made about how animals perform certain tasks with respect to environmental selection pressures, but also when such capabilities evolved. Distantly related species may show similar cognitive abilities such as tool use or social cognition, for example, corvids and apes (Emery and Clayton, 2004a, Seed et al., 2009a). Although these characteristics appear to have functional similarities, they are likely to result from very different cognitive mechanisms (Seed et al., 2009a). Traits that are not shared by a common ancestor may have converged through independent evolutionary processes (Figure 1.1). Similarly, if the common ancestor showed the trait, then it is the absence of the trait in extant species that also signifies adaptation. For example, in the case of tool use, it was recently assumed that only New Caledonian crows (*Corvus moneduloides*) habitually used tools in the wild and therefore there was something 'special' about their cognitive adaptations for tool-related cognition (Bluff et al., 2007). However, recent studies on non-tool-using rooks (*Corvus frugilegus*) have found complex forms of innovation and flexibility in the use of objects as tools, similar to that demonstrated by New Caledonian crows (Bird and Emery, 2009). Therefore, we may now assume that the common ancestor of corvids, or at least members of the *Corvus* genus, likely possessed the cognitive adaptations for object manipulation that developed into tool use—under the correct environmental conditions—for one species of crow. Reconstructing the evolutionary relatedness of species and the presence or absence of cognitive traits may therefore help clarify when cognitive adaptations arose. In this case, we need to determine whether other corvids both inside and outside the *Corvus* genus can use tools or manipulate a variety of objects in tool-related contexts in the same way as rooks, to determine when these particular adaptations may have arisen.

Another reason why a broad evolutionary approach to comparative cognition is important is because it removes anthropocentric bias. The historical focus

of animal cognition has centred on a limited number of species (Beach, 1950), specifically great apes, pigeons, and rats. However, the fundamental processes of learning and cognition are said to be the same for all animals (Pearce, 2008). By comparison, the anthropocentric approach has focused on whether supposedly unique human cognitive abilities, such as categorisation, reasoning, theory of mind (ToM), mental time travel, and symbolic communication are also found, to some degree, in other animals. More recently, comparative studies have incorporated an increased variety of species into this project (Shettleworth, 2009).

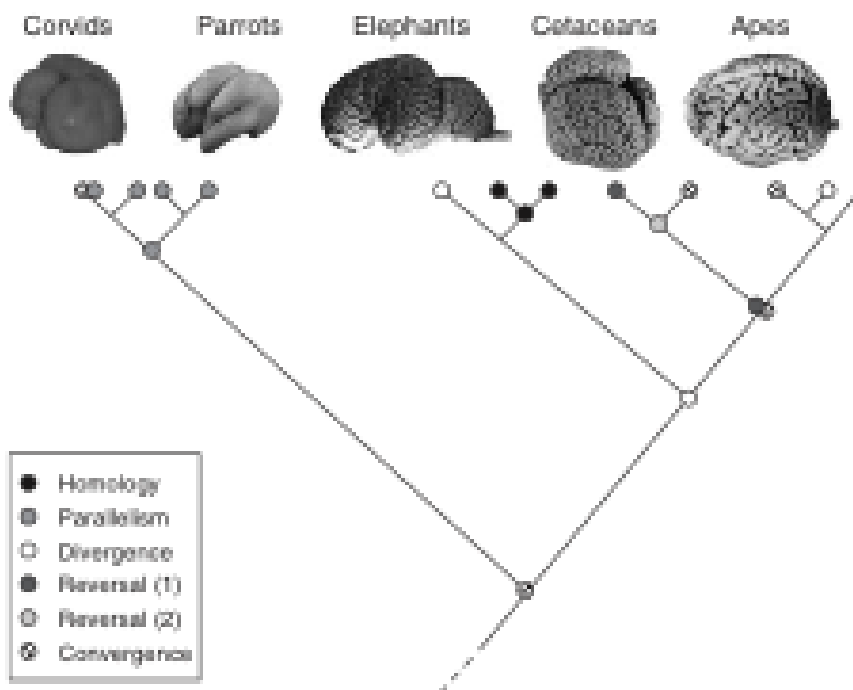


Figure 1.1: Phylogenetic trees and evolutionary principles. Schematic representation of a phylogenetic tree with relatively large-brained vertebrates—corvids, parrots, elephants, cetaceans, and apes. The circles represent the types of evolutionary principle that may govern the evolution of cognition (Sherwood et al. 2008). Homology (black circle) refers to evolution of similar traits in closely related species with a common ancestor (e.g., African elephant and Indian elephant). Parallelism (light gray circle) refers to the evolution of similar traits in relatively closely related species (e.g., corvids and parrots). Divergence (white circle) refers to the evolution of dissimilar traits by distantly related species (e.g., elephants and apes). Reversal (dark gray circle and hatched circle) refers to the evolution of a trait seen in a descendant that recovers features of the common ancestor (e.g., cetaceans). Convergence refers to the evolution of similar traits in distantly related

species (e.g., apes and corvids). Chimpanzee, elephant, and dolphin brains from Comparative Mammalian Brain Collection (brainmuseum.org). Parrot brain provided by Andrew Iwaniuk (University of Lethbridge). Corvid brain from own collection.

MAJOR THEORIES OF COGNITIVE EVOLUTION

A number of theories have posited evidence that the evolution of cognition is linked to specific aspects of species' life histories, such as sociality, qualitative relationships, culture, extractive foraging, tool use, or behavioural flexibility, yet no one all-encompassing hypothesis fits a global model. As such, it is likely that there are a number of environmental selection pressures contributing to cognitive evolution, each depending on particular species and their socio-ecological circumstances.

Social Living

The Social Intelligence Hypothesis (Humphrey, 1976) proposed that the flexible intelligent mind of primates was attributable to challenges that species experience in their social environment. This hypothesis later developed into the Machiavellian Intelligence Hypothesis, which considered social manipulation as evidence to suggest that primates perceive conspecifics as intentional agents that can be deceived (Byrne and Whiten, 1988). Later, proponents of the Social Brain Hypothesis began focusing on the relationships between social intelligence in primates and relative neocortex size (Dunbar and Shultz, 2007, Reader and Laland, 2002). Fundamental to all three hypotheses is an association between the complexities of primate social interactions and social cognition. As such, it is those animals that live in large social groups, where individuals have to keep track of the identities and interactions of numerous individuals, which have developed advanced cognitive processes. Although this view has largely been restricted to primates, other species such as cooperatively breeding birds also show comparably complex social systems. As a result, positive correlations

between relative brain size and aspects of sociality have more recently appeared in other species (Dunbar and Shultz, 2007, Emery et al., 2007). However, complex cognition among particularly social, or cooperative species may not only be confined to the social domain. While cognition may have evolved through socially mediated selection pressures, the resulting adaptations may also allow animals to solve complex problems across different cognitive domains.

Sex, Mating, and Relationships

The relationship between group size and brain size in birds is less clear. This is not surprising as birds do not reside in stable groups like primates, but form seasonal flocks, colonies, or roosts, sometimes comprising millions of individuals. Thus, brain size in birds, unlike primates, does not appear to increase linearly with social group size. Yet some birds that live in pairs or small to medium flocks, such as corvids and parrots, have relatively large brains (Emery et al., 2007). This raises the question of whether sociality, in terms of group size, is directly comparable between such distantly related species. Although intelligence in primates and birds may have arisen through convergent processes, such selection pressures may be constrained by differences in life histories (Emery and Clayton, 2004a). Primates, for example, tend to form stable polygynous groups, whereas birds are often monogamous, either forming transient pairs each breeding season or remaining in lifelong bonds with the same partner across years. The type and quality of relationships between individuals within each taxon may be equivalent, but the extent of social relationships in birds may be more relevant to a few individuals, such as in monogamously mated pairs. After all, monogamous relationships require cooperation when establishing and maintaining strong affiliative pair bonds, particularly when defending a nest site, and rearing offspring. As such, those birds with lifelong pair bonds or birds that cooperatively breed tend to have the largest relative brain size (Emery et al., 2007).

In some animals, certain ecological problems such as survival, foraging, or the rearing of offspring are more effectively solved socially than individually. Thus, it may be those mechanisms that enhance social cohesion that drive brain-size evolution rather than group size per se. However, individuals that develop stable social relationships must also face cognitive demands that solitary individuals do not (Dunbar and Shultz, 2007). But which aspects of sociality require such additional processing powers?

Cognition may play a role in maintaining long-term relationships, so called relationship intelligence (Emery et al., 2007). This is reflected in the social bonds that are established and maintained by active food giving, behavioural synchronisation, allopreening, and post-conflict affiliation. Relationship intelligence, compared to general social intelligence, focuses on the role of cooperation and coordination in dyadic interaction, allowing individuals to better read the subtleties of their partner's behaviour, thus providing a competitive edge.

Finding, Extracting, and Protecting Food

Social learning and the evolution of socio-cognitive skills also play important roles in efficient foraging strategies (Reader and Laland, 2002). Social foraging may impose greater cognitive demands than individual foraging, as it may require the ability to store and manipulate information about social relationships (Dunbar and Shultz, 2007). An awareness of other group members also presents the opportunity to acquire specific foraging techniques through direct observation of more experienced group members. Individuals may thus benefit from social learning by enhancing their efficiency in manipulating or extracting foods that would have otherwise been more difficult or harmful to obtain through trial and error learning. As such, those species that use manipulative and explorative foraging techniques are less neophobic and more innovative than other species (Day et al., 2003). Similarly, those species that adopt a generalised diet, opposed to a specialised diet, possess greater behavioural flexibility and knowledge about

food sources and foraging techniques (Reader and Laland, 2002). Thus, both social and generalised foraging behaviours may contribute to the evolution of cognition.

Species that track ephemeral food sources or retrieve food items stored in numerous locations also confront additional cognitive challenges. To efficiently locate food, frugivorous primates and food-storing birds rely on spatial and temporal abilities for learning and remembering the locations and permanence of food items that are scattered (Grodzinski and Clayton, 2010, Milton, 1988). Food-storing birds must be sensitive to their social context when caching, as their stores may be pilfered by nearby observers (Clayton et al., 2007). When storing food in the presence of potential thieves, corvids evaluate the quality of visual information available to observers and adopt strategies to reduce this information and thus minimise the risk of theft. Ravens and scrub-jays will wait until observers are distracted or cannot see them before storing food, store at further distances from observers, store behind objects, or in dark areas. Ravens and scrub-jays also use strategies that appear to tactfully deceive potential thieves such as leading them away from food stores, making false stores, or returning alone to restore food in new locations unbeknown to an observer (Clayton et al., 2007).

Technology, Tools, Innovation, and Culture

The application of flexible foraging and technical skills may be as important to the evolution of cognition as sociality (Byrne, 1997). Technical innovation and the acquisition of new food resources positively correlate with an increased brain size in both birds and primates (Lefebvre et al., 2004). Such flexibility may then be maintained or even improved through social learning and cultural transmission. Species that demonstrate proficient use and manufacture of tools show particularly complex cognitive capacities (Bluff et al., 2007, Pearce, 2008). Some corvids have demonstrated the ability to manipulate non-functional novel objects into functional tools to retrieve food rewards (Bird and Emery, 2009, Weir et al., 2002). Such innovative behaviours not only

display an accomplished perception of the problems at hand, but also suggest an understanding of the inadequacies and physical properties of available non-functional tools.

Sociality may facilitate the transmission of innovative behaviour through observation and social learning. As a result, population differences in the types of tools manufactured, like those observed in New Caledonian crows (Hunt and Gray, 2003) and chimpanzees (Whiten et al., 1999), might culminate in cultural differences. The cumulative evolution of tool complexity or foraging techniques may also provide analogous clues to the technical innovations of humans (Hunt and Gray, 2003). Is the proficient use of tools then an expression of a pre-existing physical intelligence or the result of a technological ratchet; a mechanism that provides selective pressures for further cognitive adaptations?

ALTERNATIVE VIEWS

The above views focus on evolutionarily adaptive explanations for the current functions of cognitive traits. However, the adaptive aspects of evolutionary history, as a direct result of natural selection, may not necessarily account for the causal basis of enhanced cognition. There may be other potential reasons for the origin of such traits. Complex cognition (i.e., cognitive processes that are over and above the basic psychology required by most species in order to survive) may instead be the result of nonadaptive processes that arose as a necessary by-product of other adaptations. Similarly, it may also be that complexities of a structure and its development impose restrictions on adaptive cognitive change (Gould, 1997, Gould and Lewontin, 1979). Certainly, the brain is an incredibly sophisticated structure that controls millions of different bodily processes, of which cognition is but one. However, the brain is too metabolically expensive to have resulted in a collection of traits that arose as an evolutionary accident.

New processes of evolution appear through previously existing organs or physiological activities (Lewontin, 1998). Advanced cognitive capacities may therefore have evolved as secondary consequences, or 'correlations of growth' (Darwin, 1859), that later became useful through exaptive processes (Gould and Lewontin, 1979). It is therefore important, when searching for the evolution of cognition, not to separate current utility of adaptations from their historical origin. Making inferences about the ultimate reasons for the evolution of cognitive structures or behaviours with respect to a species' current fitness may only result in speculative 'Just So Stories' (Lewontin, 1998).

IS THERE ANY EVIDENCE FOR DOMAIN-GENERAL INTELLIGENCE IN ANIMALS?

The ecological view proposes a modular approach to learning mechanisms. For example, learning about space, time, or number is attributed to specific contexts. Hence in this view, cognition is considered a collection of adaptive specialisations that are domain specific (Shettleworth, 2010). However, it is the generalisation of such adaptive processes and their application to novel tasks that confer behavioural flexibility. It is for this reason that evolutionary psychology promotes the metaphor of the mind as a Swiss Army knife; a general-purpose tool made up entirely of special-purpose devices. But the question remains whether there is a module for everything?

Cognitive adaptations may initially develop under certain selection pressures, but during the course of evolution become applicable to an expanding range of stimuli (Heyes, 2003). Can this process of generalisation, from adaptations to exaptations, promote a domain-general intelligence? Examples might be found outside of adaptive specialisations in species that may have secondarily lost adaptive traits characteristic of a common ancestor. For example, rooks and various species of monkeys do not use tools in the wild and yet demonstrate tool use and physical cognition in the laboratory (Bird and Emery, 2009, Hauser, 1997, Santos et al., 2003).

THE FUTURE OF COGNITIVE EVOLUTION

As cognitive adaptations do not fossilise, is trying to reconstruct an animal's (including human's) cognitive evolutionary history redundant? Testing evolutionary hypotheses about cognition can be difficult because cognitive processes affect fitness indirectly through behaviour. Are then any hypotheses inferring adaptation no better than mere speculations (Lewontin, 1998)? It is difficult to infer the mechanisms that drove divergence in brain size and cognition between humans and non-human apes, as all intermediate species that could provide such clues are extinct. Evidence from fossil remains of early hominids may provide useful clues, as *Archaeopteryx* did for birds and reptiles, but more rigorous tests of the relationships between adaptive behaviour and the environment are required.

Testing cognition relies on direct observation, model building, experiment, and the comparative method (Shettleworth, 2010). However, the evolutionary questions about cognition involve both the evolution of cognition and the effects of cognition on evolution. Therefore, traits must be considered as both objects and subjects of evolutionary processes—consequences of a process of change and also the cause of change (Lewontin, 1998). Tests may claim that traits are adaptive by (1) modelling how well a character serves a hypothesised function, (2) comparing whether variations of a trait correspond to variations in ecology, or (3) directly by experiment. Comparisons can be made between contrasting groups of species; those with, those without, or those possessing traits at different degrees. Measurements of the reproductive effects of variation of the trait can then be made and any genetic differences that underlie different forms of the trait can be illuminated. However, it is important to remember that any interpretations of adaptations are limited to observations of their current effects on fitness. It might be interesting to know how cognition arose, spread, and changed, but our interpretations may always be reduced to elaborate speculations, and thus we may never know.

UNIQUELY HUMAN COGNITION

This review has discussed how different species may have evolved similar cognitive abilities in response to either shared learning mechanisms or analogous environmental selection pressures. Examples such as causal reasoning in tool use, episodic-like memory of the type, state and location of food caches, and the ability to predict the behaviour of others during competition for food all suggest that a few species (e.g., apes, corvids, parrots, elephants and cetaceans) are endowed with more sophisticated cognitive capacities than other animals (Emery and Clayton, 2005). These examples appear to be related to socio-environmental traits such as complex social systems, unpredictable environments, altricial offspring, and an omnivorous diet, which are shared among these same large-brained, cognitively endowed species (Emery, 2006). Importantly, these complexities may also have been present in early hominids and so potentially responsible for driving the evolution of flexible forms of innovative behaviour in our ancestors. But do humans possess any unique cognitive abilities that do not show parallels in other animals?

Occasionally, observations of previously unexpected human-like abilities appear in non-human animals, including those that are distantly related to humans, such as teaching (Thornton and Raihani, 2008), culture (Whiten et al., 1999), recursion (Gentner et al., 2006), episodic memory (Clayton and Dickinson, 1998), and planning (Raby et al., 2007). However, it has been argued that these abilities differ between humans and animals because they are based on a profoundly different cognitive architecture (Penn et al., 2008). For example, animals do not form symbolic representations that can be used during communication and cannot reason about unobservable states (e.g., feelings and forces) rather than behaviour. An additional contrast is that these behaviours tend to be highly domain specific, relatively inflexible, and species typical. Yet it remains unclear why such abilities should be considered less sophisticated just because they are domain specific.

Although the search for human uniqueness has traditionally been sought from studies of apes (Premack and Woodruff, 1978), more distantly related species also appear to share cognitive adaptations with humans for space, objects, tools, categorisation, quantification, understanding social relationships, intentional communication, social learning, and social cognition (Emery and Clayton, 2004a, Shettleworth, 2010). But many aspects of human cognition appear to be totally unique: people communicate across continents, write poetry, perform calculus, and make wine. Therefore, the question posed is whether a small difference in our evolutionary (or cultural) history made a big difference to the human brain and cognition? In this final section, we will assess whether supposedly unique aspects of human cognition are shared with other animals.

Theory of Mind

Humans have developed unique sociocultural adaptations that enable them to pay attention to the behaviour of other individuals in their social group. This ability is thought to have developed from an understanding of others as distinct mental entities that possess beliefs and desires of their own (Andrews, 2005). In short, these processes involve concepts of mental representation or a Theory of Mind (ToM). The possession of a ToM is derived from an understanding that the behaviour of others is intentional, which can then be used to predict others' future behaviours and provide explanations for their actions (Penn and Povinelli, 2007).

To determine whether animals possess elements of a ToM, tests have focused on different categories of mental states, based on perceptual, informational, and motivational domains. For example, examining what animals know about what another can or cannot see tests their understanding that others have perceptual mental states, whereas examining what animals know about what another may know (for example, from what they may have seen in the past) tests their understanding that others have informational mental states. However, the benchmark for human ToM is testing whether

animals form concepts of false beliefs that (1) may contradict reality and (2) may be different from what the observer knows to be true (Emery and Clayton, 2009). Some animals, such as chimpanzees, dogs, and corvids show advanced predispositions to respond to certain behavioural cues, but no non-human animal has convincingly demonstrated an understanding of false belief; therefore, the possession of a true ToM may still be considered unique to humans (Tomasello et al., 2005). Only children around 4 years old have demonstrated the ability to separate their own representations of a situation from another's.

Tomasello and colleagues (2005) suggest that this socio-cognitive skill promotes uniquely human joint attentional activities and shared intentionality that form the basis for culture. Shared intentionality requires the ability to view others as causal agents and make cognitive representations of others' minds, thus providing the motivation to collaborate in shared goals. Such collaboration may thus form the basis of cultural evolution, facilitating the creation and use of linguistic symbols, the construction of social norms and individual beliefs, and the establishment of social institutions (Tomasello et al., 2005). The development of such traits further enhances their transmission across generations allowing for cumulative cultural learning and unique processes of cultural cognition and evolution.

Mental Time Travel

Mental time travel is the process of recollecting one's past information about what happened where and when (retrospection) and using this information to project one's self into the future to anticipate future needs (prospection) (Suddendorf and Corballis, 2007). Episodic memory, in contrast to semantic memory, is information about personally experienced events, rather than just knowledge of the event itself. An example may be the reconstruction of where and when, and the associated emotional responses elicited from learning that George W. Bush was re-elected, as opposed from merely knowing the fact that he won a second term. The ability to make retrospective and prospective

decisions may have direct implications for survival in the future and thus be an important component of human cognitive evolution. In a fluctuating environment, species that distinguish certain regularities based on prior experiences and adapt this knowledge to future decisions have an advantage over those that do not. The question remains whether mental time travel is unique to humans because two critical components of human mental time travel involve phenomenological consciousness, namely auto-noesis (awareness of authorship) and chronesthesia (awareness of the passage of time) (Clayton et al., 2008, 2009, Suddendorf and Corballis, 2007), which are difficult to test without the faculty of language.

Recent research suggests that apes, corvids, parids, and rats demonstrate behaviours indicative of episodic-like memory and future planning (Grodzinski and Clayton, 2010). For example, research on food-storing birds has utilised the natural caching behaviour of these animals to develop paradigms for investigating what jays may know about what they cached, where and when, who was present when they cached, as well as decisions about what and where to cache for future needs (Grodzinski and Clayton, 2010). However, it remains difficult to interpret non-verbal approaches to mental time travel and infer whether animals possess unconstrained capacities analogous to those of humans, rather than limitations imposed by instincts or conventional learning. Therefore, an approach based on behavioural rather than verbal criteria has to be adopted (Clayton et al., 2003).

Culture

Human culture has flourished as a result of identifying intentional behaviours in others. By distinguishing actions as a means to achieving underlying goals and recognising shared intentions in terms of aligning ones own goals with those of conspecifics, individuals can learn and be taught through the medium of a social–collective culture. Many animals display traits that are suggestive of culture (Hunt and Gray, 2003, Whiten et al., 1999). However, what may make human culture unique is the mechanism by which information passes

within and between social groups (Price et al., 2010). Material or symbolic artefacts can also be culturally transmitted through succeeding generations. A cumulative process ('ratchet effect') of modifying, improving, or finding new ways to incorporate an artefact into social practices then results in cultural evolution; the new and improved version gets passed onto the next generation, and so on. Successful cultural transmission not only relies on imitation and teaching, but is also facilitated by collaboration and communication (Tomasello et al., 2005). These pressures may then result in the evolution of symbolic forms of communication such as language.

Language

Some researchers claim that humans alone are capable of acquiring language and that it is this capacity that accounts for our unique intellectual abilities (Premack, 2007). There is no doubt that language has played a central role in the evolution of human cognition. However, it is clear that language is not necessary for cognition to occur. Language is the result of adaptations derived from shared intentions and group-orientated coordination and collaboration (Tomasello et al., 2005). It is those underlying cognitive and social skills that motivate people to share personal information, knowledge, and perspectives that are unique to humans. As a result, language and thought are likely to have coevolved, 'ratcheting' each other up as language created new cognitive niches.

CONCLUSION

Over the past 30 years, the resurgence in comparative cognition has dramatically extended our understanding of the human and non-human mind. Such renewed vitality has spawned many creative and imaginative studies, each furthering our insight into the evolution of cognition. Research comparing subtle differences in cognitive processes between humans and other closely related species highlights evolutionary divergences in cognitive trajectories, whereas cognitive similarities between humans, other apes, and

more distantly related species, such as corvids, highlight evolutionary convergence. For example, contemporary approaches that focus on more distantly related species such as birds have revealed previously unsuspected humanlike abilities, such as mental attribution, episodic memory, future planning, and self-awareness, further illuminating the convergent processes of cognitive evolution. We now know empirically, as Darwin once speculated, that humans and non-human animals share many fundamental cognitive abilities, yet the development of such abilities differs in degrees across species. These differences are likely to be based on different computational demands in those species' socio-ecological environments (Penn et al., 2008), and especially that of the ancestral species. Although we will never fully realise what this environment and the associated selection pressures were like, many critics suggest that this makes the study of cognitive evolution a 'scientific dead end'. We believe that comparative, phylogenetic, experimental, and theoretical tools are in place to allow us to try to reconstruct the evolution of specific cognitive traits and their neural correlates.

1.3: Convergent Evolution of Cognition

Introduction

Our understanding of the convergent evolution of cognition hinges on comparative studies among phylogenetically distinct species. This is not to say that comparative cognition is solely restricted to studies of distantly related species; comparisons between closely related species, such as humans and other primates, especially chimpanzees, also reveal compelling insights into the divergent processes of cognitive evolution (e.g., Tomasello and Call, 1997). However, the defining criterion of convergent evolution is that it occurs across distantly related species. As a result, the convergent evolution of adaptive traits can be considered to arise independent of phylogeny and shaped by common solutions to similar socio-ecological problems.

By considering cognition as an adaptive specialisation—that is, a trait that is driven by environmental selection pressures—such selection pressures can be shared among distantly related species that face similar socio-ecological challenges. As a result, analogous adaptations may evolve independently among distantly related organisms (Keeton and Gould, 1986). Any similarities in traits (i.e., cognitive abilities) can then be attributed to shared environmental selection pressures rather than to characteristics present in a common ancestor (Ridley, 1993). Consequently, the greater the phylogenetic separation between groups, the stronger the case for evolutionary convergence (Papini, 2002).

One example of convergent evolution is the adaptation of active flight among distantly related vertebrate species (Seed et al., 2009a). Birds, bats, and pterosaurs, for example, share the functional ability of flight, but lack structural similarities in their forelimb morphologies (Figure 1.2). Flight in birds evolved through the extension of the bones of the forelimb, whereas bats and pterosaurs support the wing through extended digits: the fifth digit for

pterosaurs; and the second, third, fourth, and fifth for bats. Yet, the convergent shape of the wing is the result of environmental selection pressures and the functional constraints imposed by flight.

Cognition has been described as “the mechanisms by which animals acquire, process, store and act upon information from the environment” (Shettleworth, 2010, p. 4). This chapter proposes a model of cognition as a domain-specific adaptive response to specific environmental selection pressures, which can then be generalised and applied to solve novel tasks of functional equivalence. This proposal predicts differences between species based on different adaptations for complex problem solving in the wild. An alternative hypothesis proposes that there are no qualitative differences in the processes of cognition between species (Bolhuis and Macphail, 2001), even in those species that live in different environments.

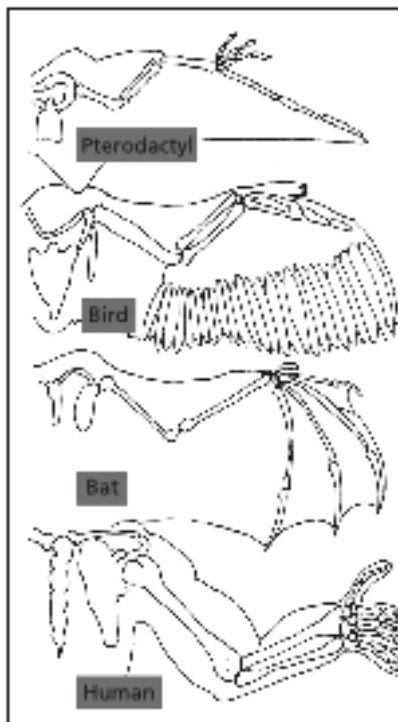


Figure 1.2: Convergent evolution of wing and arm structure in pterodactyls, birds, bats, and humans. Although the structure of the wing is different in pterodactyls, birds and bats, the resultant behaviour—flight—is the same. This may represent a parallel to convergent evolution of cognition in corvids and apes, yet with very differently structured brains.

In addition to such controversies is the debate about whether certain behaviours are, in fact, governed by so-called higher-order cognitive processes, or whether intelligent behaviour is simply the result of “hardwired”

adaptive specialisations—conserved associative learning processes (i.e., conditioning). It is, therefore, important that cognitive processes are tested by determining whether certain behaviours can be flexibly expressed across a variety of tasks of general equivalence.

COMPARING TANGIBLE TRAITS & INFERRING TANGIBLE PROXIES

Unlike wings, which can be easily dissected to reveal any structural differences in morphology, cognition is an intangible trait ascribed to an organism's psychology. Thus, comparisons may be made across species only by identifying measurable proxies that are ecologically relevant to cognitive aptitude, such as measures of relative brain size.

Brain Structure and Function

One useful proxy for intelligence is the size of specific components of an organism's brain relative to its overall body mass (Figure 1.3). Overall brain size has been criticised as a poor measure of cognitive capacity, because (1) brain size correlates with body size, and (2) many brain areas control primary, sensory, and motor functions that are not directly associated with cognition (Jerison, 1973). However, more recent studies have found that overall brain size is a better predictor of general intelligence (at least in primates) than other measures, including relative brain size and neocortex size (Deaner et al., 2007). Yet there are certain areas of the brain that are more closely associated with higher-order processing, such as the neocortex in mammals and the forebrain in birds (Striedter, 2005).

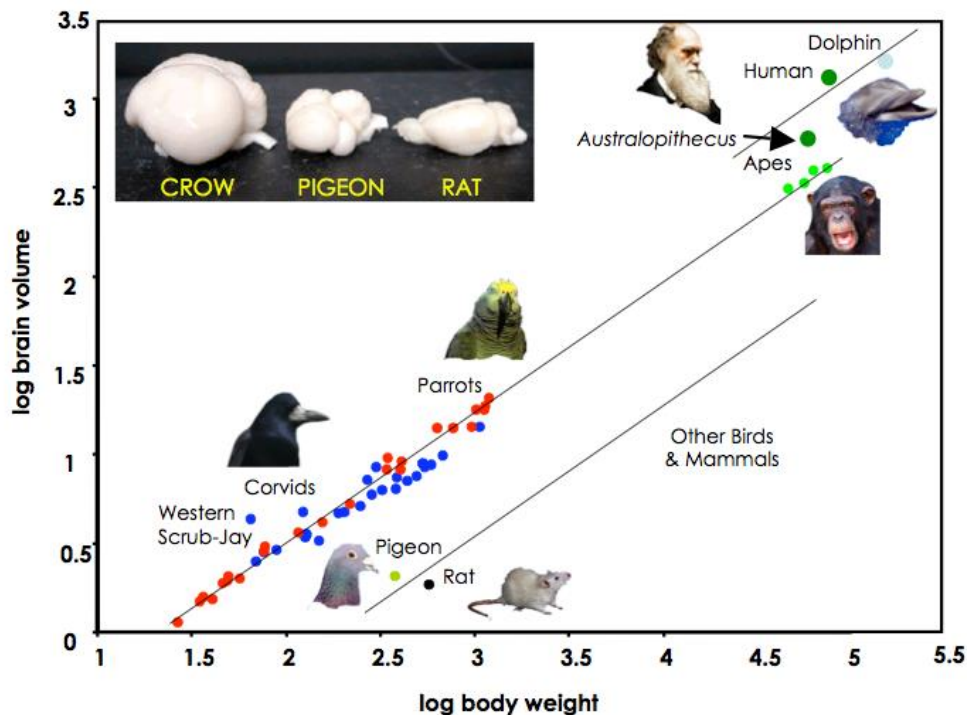


Figure 1.3: Graph of log brain volume against log body weight for a number of birds (corvids, parrots, and pigeons), mammals (rats, primates, cetaceans), *Australopithecus* and *Homo sapiens*. Data on body size and brain volume were taken from various published sources.

Jerison (1973) first proposed an index to rank the cognitive skills of species based on their relative brain size, called encephalisation quotient (EQ). Although there are obvious difficulties in making generalised comparisons across taxa that live in different environments, Jerison identified that some species are endowed with an exceptionally high EQ and, hence, a relative brain size that is much larger than would be predicted for their body mass (Jerison, 1973). Of particular interest was the finding that the relative size of the forebrain in corvids (crows, rooks, and jays) and parrots is significantly larger than those of other birds (cf. Emery and Clayton, 2004b). Corvids and parrots, in fact, possess brains that are relatively the same size as those of the great apes, and in both cases they are much larger than predicted for their body mass (Jerison, 1973). Although the issue of whether brain size reflects cognitive competence remains controversial (Striedter, 2005), it is clear that those avian species that have relatively large brains, such as corvids and parrots, also display cognitive abilities that have hitherto only

been demonstrated in large-brained mammals (primates, cetaceans, elephants), especially those with a large prefrontal cortex (Emery and Clayton, 2004a; see later).

The common ancestor of birds and mammals, a stem amniote, lived over 300 million years ago. During the course of such long independent evolutionary trajectories, corvids, parrots, and apes adapted to radically different environmental requirements, but these groups also shared similar life histories (relatively long developmental period before independence, great longevity, etc.), morphological adaptations (color vision, ability to track moving objects, fine object manipulation, etc.), and socio-ecological traits (omnivory, complex social groups, individualised relationships, etc.).

Evolutionary divergence has resulted in the independent evolution of different neuroanatomical components and structures across species. Mammalian brains, for example, are comprised of different components to those of birds, and they are organised into a laminar arrangement of neurons compared to the nuclear clusters of neurons found in avian brains (Emery, 2006). Yet analogous functions of particular brain components have been identified between these two groups (Jarvis et al., 2005). In the mammalian brain, for example, it is the neocortex that mediates cognitive processes (memory, reasoning, concept formation, and social intelligence). However, birds do not possess a neocortex. Measures of higher cognition, such as foraging innovation and tool use are, instead, identified with certain areas of the avian forebrain (Lefebvre et al., 2002), with areas analogous to the mammalian prefrontal cortex, such as the nidopallium and mesopallium (Rehkemper et al., 1991, 2004).

Although there may be fundamental differences in the size and structure of avian and mammalian brains, recent evidence suggests that both groups share advanced cognitive abilities (Emery and Clayton, 2004a). Pepperberg (1999) provides a helpful analogy: *“the structural differences between mammalian and avian brains are like the wiring and processing differences*

between IBM-PCs and Apple Macs. However, in both cases, the resulting output (i.e. behaviour or algorithmic operations) is similar.” Such similarities in cognitive traits suggest that corvid and ape cognition has undergone a convergent evolution of mental processes (Emery, 2004, Emery and Clayton, 2004a, Seed et al., 2009a). In fact, many animals demonstrate intelligent behaviour, suggesting that cognition may have evolved independently among several vertebrate groups, including great apes (Tomasello and Call, 1997), corvids (Emery and Clayton, 2004a), cetaceans (Marino, 2002), hyenas (Holekamp et al., 2007) and canids (Hare and Tomasello, 2005, Miklosi et al., 2004), among others (see later).

Is Cognition Similar in Different Species?

Not only do corvids and apes appear to possess analogous neuroanatomical components responsible for cognitive processes, but they may also share similarities in how they form representations of their social and physical worlds. Thus, it is in the recognition of shared socio-ecological challenges that species face in their day-to-day lives that convergent adaptations may be revealed. For example, recent research has revealed evidence that corvids demonstrate similar reasoning abilities as great apes, with regard to how tools work, how social agents can be manipulated, and how events are remembered (cf. Seed et al., 2009a).

Recognising behavioural similarities shared among different species provides a basis for inferring similarities in cognition. For example, using tools to aid in extractive foraging may not only be an adaptive response to acquiring an otherwise inaccessible resource, but proficiency might also be refined over time through social learning. However, it is only by going beyond the broad observations, such as that both apes and corvids are capable of tool manufacture, that information about *how* these species process such information can be revealed. For instance, what range of problems are these animals capable of solving? Do they make or use tools for particular purposes, adapting or modifying them depending on their context of use?

Does a species' understanding of how tools work depend on causal reasoning or other psychological processes? Only by conducting experiments using comparative methodology can we explain limits to such similarities and thus establish the convergent processes of cognitive evolution.

Species with dramatically different life histories, morphologies, brain structures, and ecologies may perceive the world quite differently from one another. For this reason, it is important to consider the ecological validity of comparative tests. Attempts to make direct comparisons of psychological processes across phylogenetically distinct species may be marred by species-specific differences in perception, attention, and motivation (Bitterman, 1960, 1965).

An organism's neuro-architecture is influenced by adaptations to specific environmental selection pressures. For instance, there may be differences in the environmental constraints imposed on brain size among aquatic species compared with aerial species. Moreover, species' life histories may also result in more subtle variations. For example, migratory birds that spend much of their life in flight may be subjected to tighter energetic constraints and, thus, tend to possess significantly smaller brains than those of sedentary or nomadic species (Burish et al., 2004). The occurrence of cognitive traits may also be more likely to evolve among certain species. For example, the manufacture and use of tools is more frequently observed in great apes than in birds. This may be because birds possess a multifunctional beak, thus rendering the manufacture of tools unnecessary in many of the foraging challenges that birds encounter.

PREREQUISITES FOR INTELLIGENT BEHAVIOUR

Cognition is thought to have arisen independently across distantly related species through processes of convergent evolution, driven by the need to solve comparable social and ecological problems (Emery and Clayton, 2004b, 2004b, Marino, 2002, Seed et al., 2009a). Such environmental challenges

often require the ability to respond flexibly by generalising domain-specific behaviours (i.e., behaviours evolved to solve specific problems), and applying this knowledge to accommodate for more broad and variable interactions that species encounter in their environments. As a result, behavioural flexibility is often attributed as an indicator of intelligence.

Corvids have consistently demonstrated cognitive skills that surpass those described in other birds, and in many cases they rival similar cognitive domains previously thought confined to monkeys and apes (Emery, 2004, Emery and Clayton, 2004a, 2004b, Seed et al., 2009a). Similarities among species' life history traits may, therefore, provide clues to cognitive aptitude. Corvids and parrots share with the great apes, many of the biological, ecological, behavioural, and psychological attributes thought fundamental to complex cognition. Each of these aspects will be discussed in the following sections outlining any similarities and discrepancies between groups. Both corvids and parrots, for example, possess forebrains that are relatively the same size as apes; experience a long developmental period before becoming independent from their parents; are long-lived, omnivorous extractive foragers; and live in complex social groups—all socio-ecological attributes that have long been suggested as prerequisites for intelligence in primates (Byrne and Whiten, 1988, Humphrey, 1976).

It is likely that each of the socio-ecological attributes described later corresponds with differences in domain-specific cognitive abilities. That is, different species may reveal different adaptive responses in response to particular challenges in their environment. Chimpanzees, for example, use tools more frequently than their closely related cousins, bonobos, and hence, possess a more sophisticated understanding of physical causality or "*folk physics*" (Herrmann et al., 2010). Yet, those species with the most advanced cognitive abilities are likely to incorporate a number of these socio-ecological attributes (Emery, 2006), although the question that remains to be answered is to what degree these socio-ecological pressures correlate with cognitive flexibility and how these pressures are reflected in the underlying cognitive

systems of animals, which we are still far from knowing.

Biological Similarities

In this section, we highlight a number of shared biological features found in corvids, parrots, and apes, however, we are aware that these are general claims and that some of the traits are shared with other animals. The function of this section is to highlight those features that are shared by these taxonomic groups and may contribute to the similarities in behaviour and cognition we will describe in later sections.

Parenting Development and Lifespan

Ontological differences among species reveal important trends in the evolution of relative brain size, particularly between altricial and precocial species. Altricial species are born into the world blind, helpless, and utterly dependent on parental care. Yet precocial species are immediately capable of surviving independently. Such stark differences in juvenile development may appear at odds with initial survival success, yet they foretell strategic differences in species' life histories.

In birds, altricial hatchlings possess significantly smaller brains relative to their body size than precocial hatchlings (Bennett and Harvey, 1985). However, altricial adult birds possess significantly larger brains relative to their body size than precocial adult birds (Starck, 1993, Starck and Ricklefs, 1998). These findings suggest that the majority of neural development occurs in birds during an extended post-hatching period, rather than during incubatory periods. However, prolonged periods of development, whether during the incubatory period or post-hatching period, are, in fact, correlated with increases in relative brain size (Iwaniuk and Nelson, 2003). Thus, extended developmental periods and longer durations of parental care correlate positively with relative brain size (Ricklefs, 2004). A similar picture emerges for the great apes. Apes are also an altricial species, displaying a slow rate of

development, with substantial increases in brain size in the post-natal period. Indeed, there is also a clear relationship between length of juvenile period (and age at maturation) and relative brain size in primates (Ross, 2004).

Relatively extended periods of juvenile development may serve to accommodate the acquisition of knowledge, either by social learning from adults to offspring or individual learning based on trial-and-error. Acquiring such information may be particularly useful when learning about how to survive in unpredictable environments. Although this hypothesis is attractive, there is little data to support such a claim. Indeed, there is no correlation between environmental complexity (social, physical, dietary, ecological, and climatic uncertainty) and brain size in primates when controlling for postnatal growth rates (Ross, 2004). While the developmental period of corvids and parrots is relatively long compared to other birds, it remains relatively short compared to apes (Iwaniuk et al., 2003, Iwaniuk and Nelson, 2003). Life experience may therefore also influence cognitive capacity, with long-lived individuals accumulating greater knowledge through experience, while using such knowledge to make better decisions and be better prepared to respond to future problems.

Dexterity

Species equipped with grasping or dexterous limbs (primates) or generalised all-purpose beaks (birds) may be better equipped to solve physical tasks than those species that cannot easily manipulate objects. Parrots, for example have particularly dexterous grasping feet, which they effectively use to manipulate food. Similarly, primates possess hands and feet that can be used to manipulate objects. Corvids tend to use their beaks as tools, suitable for prying open, digging, puncturing, and crushing a variety of food sources, as well as a number of fine manipulations. Such a number of flexible movements allow these groups to exploit objects in their environment unavailable to other groups, which in turn require additional levels of neural and cognitive processing power not seen in other species without such dexterity.

Visual Acuity

Among primates, brain size is positively correlated with visual specialisation (Barton, 1998). In fact, the primate neocortex is comprised of about 50 percent of visual areas, allowing for accurate and high-resolution processing (Van Essen et al., 1992). High visual acuity may be particularly beneficial to primates and birds because it may enhance their ability to detect ripe fruits and moving insects, as well as predators. The relatively large brains of frugivorous primates, as opposed to folivorous species (Clutton-Brock and Harvey, 1980), may thus have resulted from selection pressures acting to enhance the detection of edible fruits using specific visual cues such as color. In addition, visual acuity may allow for the detection of social information, such as facial expressions and the gaze direction of conspecifics (Barton, 1996). Thus, it is not surprising that there is a strong relationship between the size of the visual system and socio-ecological variables such as diet and social group size in primates.

Birds are also highly visual animals (Hodos, 1993), processing color information in a greater frequency range than mammals (including ultraviolet), as well as rapidly processing movement and environmental information (Martin, 2012). However, the eyes of birds and mammals are quite different, although the central neural systems are relatively similar (Husband and Shimizu, 2001). We may, therefore, predict a similar relationship between the visual system and socio-ecological variables in birds. Indeed, in the case of prey capture, there is a co-evolutionary relationship between eye size and brain size (Garamszegi et al., 2002).

Brain Size

The relative size of corvid, parrot, and ape brains are equivalent in terms of brain size to body size (i.e., are found on the same regression line; Emery and Clayton, 2004a). An enlarged brain is metabolically expensive (Aiello and Wheeler, 1995). Thus, it is generally accepted that there must be

correspondingly powerful adaptive benefits from brain enlargement. Understanding the origins of this specialisation, therefore, becomes a question of what selective pressure(s) favoured enlarged components of the brain during the course of evolution (Isler and Van Schaik, 2009).

As discussed earlier, the relative size of specific components of an organism's brain can be used as a direct proxy to inferring higher cognitive facilities. However, it is important to recognise that any interpretations must be made with caution, because different assumptions and methodological approaches can easily distort species-wide comparisons (see Healy and Rowe, 2007).

ECOLOGICAL SIMILARITIES

Unpredictable Environments

The most recently evolved genera of corvids (*Corvus*, *Pyrrhocorax*) and apes (*Pan*) appeared at roughly the same point in evolutionary time (5–10 million years ago) during the Late Miocene and Pliocene epochs (Emery, 2006, Potts, 2004). This period is characterised by dramatic environmental and climatic variability and instability as a result of numerous ice ages. Such environmental changes would have strongly influenced food availability and consequently species' foraging strategies.

During evolutionary history, the abundance of resources may have fluctuated, becoming less reliable and irregularly distributed through time and space. Food scarcity may have been alleviated by the evolution of foraging techniques to exploit new resources. However, species that are governed by rigid stimulus-response action patterns or hardwired behaviours may not respond as well to such changes as those species that adopt flexible behaviours based on more abstract knowledge (Seed et al., 2009a). As such, extracting food hidden within encased substrates or procuring meat as an energy-rich food source may have become incorporated into species' foraging

repertoires. Thus, environmental variability may have selected for certain species to adopt innovative, omnivorous, and generalist foraging techniques, powered by increases in relative brain size (Lefebvre et al., 2004). Such ecological variables have been suggested as important evolutionary drivers of great-ape cognition (Potts, 2004); similar conditions may also be responsible for the evolution of avian (corvid and parrot) cognition (Emery, 2006), as well as other species living in such changeable environments, such as cetaceans (Marino et al., 2007) and elephants (Byrne and Bates, 2009).

One important feature of an unpredictable environment is the source of food. Foods that are ephemeral, that have to be hunted, that appear at certain times of the year, that are distributed in clumps or need to be extracted from casings, will require more cognitive abilities to obtain (e.g., spatial memory, planning, cooperation) than foods that are available all year, located in the same place, and which require little processing, such as foliage.

Generalised Diet

Many corvids, parrots, and primates are omnivorous, generalist foragers. Rooks, in particular, consume over 170 species of plants and animals, including many different parts of plants, insects, worms, seafood, birds' eggs, small vertebrates, and carrion (Cramp and Perrins, 1994). However, rooks acquire the majority of their diet through extractive foraging techniques; digging in the soil for grain, invertebrates, roots, and tubers (Lockie, 1955). Some corvids also use their beaks to hammer and pry open the hard cases of nuts such as walnuts and acorns, and drop mussels, limpets, and bone from the air until their encased contents are released.

Parrots also consume a wide variety of seeds, fruits, and flowers (Juniper and Parr, 2003). Some species, such as the kaka frequently consume insects (Moorhouse, 1997), use their large, down-curved bills to tap sap from trees and excavate grubs from both live and dead wood (Beggs and Wilson, 1987). Another New Zealand parrot, the kea, renowned for its extreme neophilia and

advanced intellect (Huber and Gajdon, 2006), is also known to consume a varied diet, including over 40 plant species (Clark, 1970) as well as discarded fat, protein, and carbohydrate-rich foods found in human settlements (Diamond and Bond, 1999, Gajdon et al., 2006). The kea is also notable as the only carnivorous parrot known for attacking sheep and eating fat from the back of the animal (Benham, 1906, Diamond and Bond, 1999), as well as excavating sooty shearwater chicks from their underground nest burrows (Cuthbert, 2003). Utilising such a variety of food sources is a likely response to living in mountainous regions characterised by a harsh and unpredictable climate, resulting in an irregular food supply. It is not yet clear whether the seemingly more complex dietary habits of keas, when compared to other parrots, is reflected in their physical cognition (Liedtke et al., 2010).

Seeds are a more common component of parrots' diets, but many seeds have a hard case, requiring dexterous manipulation to extract their contents, preventing most other arboreal foragers access. Some parrots, for example hyacinth macaws (Borsari and Ottoni, 2005) and black palm cockatoos (Wallace, 2000), proficiently open hard-cased seeds by using wedge-like pieces of wood or leaves as tools to better grip nuts with their upper mandible, and, while holding the nut in place with one foot, open the hard casing with their lower mandible.

Primates also demonstrate skilful extractive foraging techniques, the most prominent example being termite fishing by wild chimpanzees (Goodall, 1963, van Lawick-Goodall, 1968). However, chimpanzees (Boesch and Boesch, 1990) and capuchins (Fragaszy et al., 2004) also crack hard-cased nuts with hammers and anvils to extract their contents. Although such behaviours are commonly observed, termite fishing and nut cracking require sophisticated manipulation and dexterity to succeed. Chimpanzee infants require years of observation to learn how to make tools (Biro et al., 2003, Lonsdorf, 2006). Similarly, capuchins' success at nut cracking varies considerably between individuals and is likely to require years of practice to attain an efficient technique (Fragaszy et al., 2010).

Extractive foraging may have evolved in response to food scarcity. Species that evolve novel foraging techniques may exploit niches that are not readily available to others, often containing energy-rich foods that are high in nutritive value and available throughout the year. In addition, extracting encased foods often requires a variety of complex sensorimotor skills for locating and manipulating food items. Such processes have been suggested to provide support for the evolution of intelligence in apes (Parker and Gibson, 1977), although other studies on primates found no relationship between extractive foraging and neocortex ratio (Dunbar, 1995).

Foraging in Space and Time

The main foods consumed by corvids, parrots, and primates (fruits, seeds, and invertebrates) are often patchily distributed through space and vary in their temporal availability. Other species may also face similar challenges in locating food items, such as cetaceans' diet of fish, krill, and cephalopods, which may be equally variable in abundance and distribution (Marino, 2002). However, such temporal and spatial patchiness may be predictable; plants remain in the same place and fruits often ripen at predictable intervals. Likewise, regularities in ocean currents or seasonal spawning times may allow cetaceans to predict the location and timing of abundant food supplies.

Yet closely related species can differ substantially in their dietary requirements and hence foraging strategies. Some primates rely on a varied diet of fruits, whereas others predominantly consume leaves. Leaves are, however, considerably more abundant than fruits, and their distribution is regular. Frugivorous primates are, therefore, faced with an additional challenge; locating an ephemeral and patchily distributed resource. However, primates that remember the locations and fruiting patterns of a variety of plant foods might improve their foraging efficiency (Janmaat et al., 2006). Selection pressures, favouring foraging efficiency, are, therefore, thought to enhance species' cognitive capacities for spatial and temporal memory (Milton, 1981). As such, cerebral expansion is more pronounced in frugivorous primates,

rather than folivorous species (Clutton-Brock and Harvey, 1980).

Some animals have evolved specialisations for remembering and predicting the location of resources that are irregularly distributed through time and space. The most extensively documented accounts of such behaviour come from experiments on spatial memory in food-caching animals (Vander Wall, 1990). When an abundant food supply is available, many animals store food for consumption in later periods of food scarcity. However, to efficiently recover their caches, storers need to process information relating to the location of their cache sites, the type, and perishability of stored food items, and the social context of caching (Clayton et al., 2007, Clayton and Dickinson, 1999, van Horik and Burns, 2007). Some corvids, such as Clark's nutcrackers, can cache up to 30,000 pine seeds over large areas, recovering a majority of them up to six months later. Such behaviours suggest that these birds possess a proficient long-term spatial memory (Balda and Kamil, 1992). Conversely, other corvids, such as Western scrub jays, cache fewer but a wider variety of food items that differ in their rates of perishability. Consequently, Western scrub jays not only remember where they cached, but also what they cached and when, so that perishable food can be recovered when it is still edible (Clayton and Dickinson, 1998, 1999, Clayton et al., 2001, 2003, de Kort et al., 2005).

BEHAVIOURAL SIMILARITIES

Tool Use and Manufacture

Recently thought to be uniquely human, the first report of tool use outside of humans was in wild chimpanzees (van Lawick-Goodall, 1968). We now know that many species of insects, fish, birds, and mammals use tools in the wild (Beck, 1980, Emery and Clayton, 2009b). However, in the wild, only chimpanzees, orangutans, New Caledonian crows, and woodpecker finches habitually use and manufacture tools during their daily foraging activities (Hunt, 1996, Tebbich et al., 2002, Tomasello and Call, 1997, van Schaik et

al., 2003). Yet the extent to which these animals understand how tools work, that is, their physical properties and the unobservable forces that govern their function—so-called *folk physics*—remains controversial (Emery and Clayton, 2009b, Povinelli, 2000).

Tool use requires “the use of physical objects other than the animal’s own body or appendages as a means to extend the physical influence realised by the animal” (Jones and Kamil, 1973 p. 1076). Hence, Egyptian vultures (*Neophron percnopterus*) that crack open eggs by dropping them onto rocks do not demonstrate tool use, whereas vultures that throw stones (as a physical extension of their body) to open eggs fit these criteria. Likewise, the examples of corvids dropping mussels to crack open their hard shells, thrushes that open snail shells by smashing them onto stones (Gibson, 1986), or crows in Japan and California that open hard-shelled walnuts by dropping them from great heights onto hard-surfaced roads (Cristol and Switzer, 1999, Nikei, 1995) do not demonstrate tool use when discussed in terms of the earlier definition. However, manipulating encased food items to extract their contents (extractive foraging) requires certain forms of cognition, particularly when compared with nonextractive forms of foraging.

Although most species of great apes make and use tools, the most proficient primate tool user in the animal kingdom is the chimpanzee (Tomasello and Call, 1997). Yet there have also been numerous reports of tool use in birds, especially corvids (Lefebvre et al., 2002). One of the most striking applications of tool use by any animal can be observed in wild New Caledonian crows. These birds routinely use and transport manufactured tools during daily foraging expeditions, and they use different types of tools depending on their functional requirements: stepped-cut Pandanus leaves are used in a rapid back and forth fashion to search for prey under leaf litter, whereas hooked twigs are used to extract insect larvae from within tree cavities using slow deliberate movements (Hunt, 1996).

Both New Caledonian crows and chimpanzees manufacture tools, either fashioning probing sticks by stripping off smaller twigs and leaves from larger twigs and then inserting them into termite mounds, making hook tools by removing a series of side twigs from a larger twig and then chiselling away at a breakage point to create a hook, or cutting steps into a Pandanus leaf to make a pointed and rigid tool for rooting out grubs living under the bark of dead trees (Hunt et al., 2006, Hunt and Gray, 2004, Sanz et al., 2004). In all these cases (and others not described here), the toolmaker starts to create a tool from raw material (twigs, leaves, etc.) by removing or sculpting parts of the raw material that is non-functional as a tool, into a functional tool. Although we know little about the psychology of tool-making, this ability suggests that the toolmaker may have an image of the final tool in mind before it is made.

Sociality

Observations of social interactions among captive chimpanzees first prompted the hypothesis that social living and, thus, the challenges that species face in their social environment play important roles in the evolution of a flexible and intelligent mind (Social Intelligence Hypothesis: Humphrey, 1976). This hypothesis was later recognised as a key component of primate cognition, attributing social intelligence to the recognition and subsequent manipulation, coordination, and deception of individuals within a social group (Machiavellian Intelligence Hypothesis: Byrne and Whiten, 1988). Further support for these theories was later found in positive correlations between social-group size and neocortex size in primates (Social Brain Hypothesis: Dunbar, 1998), and cetaceans (Marino, 1996). The rationale behind these theories is that selection favours those animals that proficiently keep track of the identities and interactions of numerous individuals within large social groups. Over evolutionary time, this process resulted in the refinement of social cognition as an adaptive specialisation.

Although there appears to be a clear indication that group size has played a significant role in the evolution of brain size in primates, similar relationships are not shared among birds (Emery et al., 2007). Such differences may, therefore, be attributed to the structure of social groups. For example, primates form polygynous social groups, whereas birds are often monogamous, forming life-long pair bonds. Moreover, group size in primates may be relatively stable, yet there can be considerable seasonal variation in birds' flock size. Similar correlations between relative brain size and certain aspects of sociality have, however, been identified in some avian species such as corvids (Emery et al., 2007). Social intelligence in birds may have thus evolved in response to the requirements of maintaining relationships and coordinating cooperative behaviour within monogamous pairs, rather than having been driven by the need to manage competitive interactions imposed by group living as in primates. In other words, it may be the quality rather than the quantity of relationships that are important for birds (Emery et al., 2007). In socially monogamous birds, an increase in the quality of parental care may lead to increasing payoffs; more experienced pairs (those that have paired for more than one breeding season) may raise more chicks. As such, comparisons between brain size and mating system in birds have revealed that the largest relative brain sizes are found among long-term monogamous species and cooperative breeders (Emery et al., 2007).

Species that live within fission-fusion societies are presented with the additional cognitive challenge of adjusting to dynamic social changes, resulting from the movement of numerous individuals into and out of groups at various times (Aureli et al., 2008). Rooks, for example, congregate in large colonies during the breeding season; then, after they have raised their offspring, each breeding pair will disperse to form smaller foraging groups. Similar social structures are exhibited across a number of distantly related species that demonstrate high levels of sociality and social complexity such as chimpanzees (Goodall, 1986), cetaceans (Connor et al., 1998, Marino, 2002, Smolker et al., 1992), and possibly some corvids (Emery, 2004).

Relationships

Many animals not only recognise individuals within a group but also understand intragroup relationships, such as kinship and the social status of individuals relative to other group members (e.g., dominance rank). Such interactions become particularly clear during disputes over food or mates. During disputes, animals may recruit support from bystanders or relatives to form alliances; however, supporting a loser may prove costly. Therefore, it pays to recruit and support high-ranking individuals as well as consider the strength of pre-existing intra-group alliances. Making such decisions relies on the possession of a detailed understanding of third-party relationships (Schino et al., 2006, Silk, 1999), however, heuristics such as “always recruit the most dominant animal” may also explain behaviour consistent with that of third-party recognition (Range and Noe, 2005).

Until recently, third-party relationships were considered a unique attribute of primate cognition (Tomasello and Call, 1997). However, many mammals, such as elephants, whales, dolphins, and hyenas, form long-lasting groups that are comprised of similar kin and dominance networks to those of primates (Connor, 2007, de Waal and Tyack, 2003, Holekamp et al., 2007). Like primates, hyenas support conspecifics engaged in agonistic interactions. Engh and colleagues (2005) observed that in most disputes, the aggressor was the more dominant individual. As such, support from conspecifics was usually directed toward the more dominant individual, possibly confirming a “join the aggressor” rule of thumb, rather than specific knowledge of an individual’s relative rank. However, in a minority of cases, when a subordinate attacked the dominant, joiners also supported the dominant, suggesting knowledge of the relative rank of each individual (Engh et al., 2005).

After disputes, hyenas (Engh et al., 2005) and primates (Tomasello and Call, 1997) are more likely to redirect their aggression toward relatives of a former opponent rather than other low-ranking individuals. This suggests a knowledge of kin ship, dominance, and third-party relationships. However,

these findings may be biased because of close proximity of relatives and hence increased interactions. To further test this, Holekamp and colleagues (2007) played back distress calls of hyena pups and found that both mothers and nearby relatives of the calling cubs were more likely to elicit a response than unrelated individuals. Moreover, the dominance rank of the mother also influenced the looking of others. Together, these results provide support for kin, dominance, and third-party recognition in hyenas.

Captive rooks and jackdaws also form long-term alliances with other group members, sometimes irrespective of sex or kinship (Emery et al., 2007). Relationships in young rooks and jackdaws are thought to be initiated by food sharing, demonstrated by the unsolicited transfer of food from one individual to another (active giving; de Kort et al., 2003), which is considered an essential component of pair formation (von Bayern et al., 2007). Alliances in corvids and apes are maintained through the use of affiliative behaviours, such as allopreening and grooming, respectively (de Waal and Luttrell, 1988, Emery et al., 2007, Seyfarth and Cheney, 1984).

Rooks that form pairs enhance their individual dominance rank compared to those that remain single (Emery et al., 2007). Enhanced dominance in turn provides associated benefits such as increased food acquisition. Emery, and colleagues (2007) also report that rooks are sensitive to third-party relationships, as they redirect aggression to the partner of an individual that they have received aggression from. Furthermore, rooks engage in third-party affiliation with their partner (i.e., bill twining) after conflicts with other group members, however, unlike primates, they do not reconcile with former opponents (Seed et al., 2007). Cooperative coalitions are often observed in many social species. Female primates and cetaceans for instance, demonstrate alloparental care—“babysitting” or staying within close proximity to unrelated juveniles (Marino, 2002, Nicolson, 1986). Chimpanzees (Uehara, 1997), bonobos (Hohmann and Fruth, 2008), whales (Hain et al., 1982, Jurasz and Jurasz, 1979), and dolphins (Leatherwood, 1975, Wursig and Wursig, 1980) all exhibit cooperative feeding strategies that require

coordinated efforts of individuals within a group to capture prey. Male chimpanzees (Watts, 1998, Wrangham, 1999) and bottlenose dolphins (Connor et al., 1992) also form cooperative alliances or coalitions for the purposes of intergroup aggression (“warfare”) and mate guarding. Recently, brown-necked ravens have been shown to also use cooperative hunting, with individuals taking different roles when hunting large lizards (Yosef and Yosef, 2009).

Innovations

To accommodate rapid changes in their environment, some animals may behave flexibly by adopting innovative techniques to solve novel problems. Overcoming such challenges may require species to possess advanced cognitive mechanisms to process and manipulate environmental information, resulting in enlarged components of the brain (Dunbar, 1992). Comparing relative brain size with measures of behavioural complexity across species has revealed some of the most compelling evidence linking the evolution of brain and cognition (Lefebvre et al., 2004, 1997).

Ethologists have long observed the complex and flexible behaviours performed by animals in the wild, documenting the emergence of novel behaviours and publishing anecdotal reports as short notes in scientific journals. Reports of such innovations have been collated across numerous species and used to produce measures of species’ behavioural plasticity (Lefebvre et al., 2004, 1997). Accounts of innovations, in terms of their relative frequencies of occurrence (innovation rates), have been compared across species and found to correlate positively with relative brain size in birds and primates (Lefebvre et al., 2004, 1997), with corvids, parrots, and apes at the forefront of innovative groups (Seed et al., 2009a). Similar relationships between the observed frequency of tool use in birds and relative brain size have also been identified (using the same method of collating anecdotes; Lefebvre et al., 2002). Likewise, the relative size of the “executive brain” (neocortex and striatum) in primates has been found to correlate

positively with the number of reports of innovation and tool use in primates (Reader and Laland, 2002).

PSYCHOLOGICAL SIMILARITIES

Social Reasoning

Sociality is thought to have played an important role in the evolution of intelligence (Byrne and Whiten, 1988, Dunbar, 1998, Humphrey, 1976, Jolly, 1966). As such, individuals within a group may gain a competitive advantage (and fitness benefits) through the use of social cognition (Humphrey, 1976). It has, thus, been proposed that the recognition of other group members as intentional agents, which possess individual beliefs and desires, independent of one's own, provide the basis for complex social interactions (Tomasello and Call, 1997).

Terms such as “chimpanzee politics” have been used to describe the sophisticated social interactions of primates (de Waal, 1982), especially involving cooperation, alliance formation, social manoeuvring, manipulation, and deception. However, such complex “political” interactions may not be restricted to primates, because similar behaviours have also been observed in numerous species such as corvids (Emery et al., 2007), cetaceans (Marino, 2002), and hyenas (Holekamp et al., 2007). Evidence from such a wide variety of distantly related species further supports the theory of an evolutionary convergence of social cognition.

One of the consequences of social living is that individuals within a group are likely to forage in the same areas for the same resources, thus resulting in direct competition. For instance, chimpanzees naturally compete over food (Tomasello and Call, 1997), although in certain circumstances food sharing does occur: from mother to infant, or when close associates share prey that cannot be monopolised by any one individual, such as a monkey killed during a cooperative hunt (Uehara, 1997).

Often resources may be irregularly distributed and found in aggregated patches. Hence, when foraging in a group, it may be advantageous for individuals to be vigilant of where other group members are successfully locating food. Likewise, competition may pose risks of food theft or displacement from abundant food supplies by more dominant individuals. Thus, animals that know what conspecifics can and cannot see may benefit by using this knowledge in food competition situations.

Hare and colleagues (2000) tested this theory by presenting chimpanzees with two pieces of food placed in an arena; the subordinate chimp could see both pieces of food, whereas the dominant chimp could see only one. Because dominant chimpanzees monopolise resources, the only way for the subordinate to gain any of the food was to obtain the food that the dominant could not see. When released into the arena, subordinates typically adopted this strategy, however, there are some discrepancies in the interpretation of these results (see Karin-D'Arcy and Povinelli, 2002).

A series of controls that allowed subordinates a head start in retrieving the food further revealed that subordinates were not responding to the approach behaviour or gaze direction of the dominants (Hare et al., 2000). This suggests that the subordinate's decision about which piece of food to obtain was dictated by their understanding of what the dominant could or could not see. However, an alternative explanation is that the subordinates based their decision of where to forage on their memory of where the dominant was looking before the barrier was raised (i.e., where the dominant was looking before they made an approach movement; Povinelli and Vonk, 2004).

In subsequent experiments, Hare and colleagues (Hare et al., 2001) further investigated what chimpanzees know about what others know (i.e., what others have and have not seen in the immediate past), by manipulating (1) whether a dominant individual could see where the food was hidden, (2) misinforming the dominant's knowledge, and (3) replacing informed dominants with uninformed dominants. The findings of this study suggest that

chimpanzees can recall what another conspecific had and had not seen in the immediate past, and attribute specific knowledge of events to particular individuals (Hare et al., 2001). Although widely cited, this study is not without its critics who suggest that the chimpanzees' behaviour does not have to be the result of mental attribution; rather, it only needs to be based on sophisticated behaviour-reading (Emery and Clayton, 2009a, Karin-D'Arcy and Povinelli, 2002, Povinelli and Vonk, 2004).

Other examples of conspecific perspective taking and knowledge attribution are illustrated in experiments on food-caching corvids. Many birds and mammals hide food for future consumption (Vander Wall, 1990). However, storing food poses the risk of theft, especially if the storer cannot defend their caches. In species that forage in social groups, theft from conspecifics may be particularly accentuated. Corvids, for example, have an excellent observational spatial memory and observe one another's caching behaviour to accurately locate others' stores and pilfer their contents at a later time (Bednekoff and Balda, 1996a, Bednekoff and Balda, 1996b, Bugnyar and Kotrschal, 2002, Clayton et al., 2001), even if caches were made from a completely different perspective (Watanabe and Clayton, 2007). As such, corvids have evolved numerous strategies to reduce the probability of their caches being stolen by others (Dally et al., 2006). Corvids readily cache in lab aviaries, basing their caching decisions on the presence or absence of conspecifics (Emery and Clayton, 2001). Under solitary conditions, birds do not apply cache-protection strategies. However, when conspecifics are present, birds attempt to reduce the amount of information available to observers by caching in places that are either difficult for the observer to see (i.e., further away or behind barriers; Dally et al., 2005) or where the information of cache location is visually degraded (i.e., in dark places; Dally et al., 2004). Storers also move their caches from locations observed by potential thieves to places unbeknown to thieves, and they appreciate that different individuals have seen different events. Whether these differences are based on different knowledge states (i.e., knowledgeable or ignorant) is debatable (Emery and Clayton, 2008). Similar studies have also revealed that

ravens can discriminate between human and conspecific competitors based on differences in the information they have been given access to (Bugnyar and Heinrich, 2005). Although studies on cache-protection strategies in corvids reveal similar findings to studies on food competition in chimpanzees, both groups, for example, appear to appreciate the perspectives of others, and it remains unclear whether such findings are based on reading the behaviour of others or reading their mental states.

The strongest cue representing what others see and where others are looking is the direction of their eye gaze. Perceiving such a cue may be particularly valuable for social species with immediate adaptive benefits, such as locating food sources, predators, and mating partners. Although primatologists in the field have long suspected that primates respond to the presence of gaze cues in conspecifics (Emery, 2000), Emery and colleagues (1997) were the first to experimentally test this behaviour in the context of gaze following. They found that captive rhesus monkeys reliably followed the gaze direction of conspecifics toward target objects, ignoring distractors of the same object. The extent to which nonhuman species utilise gaze cues to locate food or infer mental states, rather than following gaze, is controversial (Emery and Clayton, 2009a). It is clear that both corvids and apes follow the gazes of a human experimenter, but they also reposition themselves to follow the experimenter's gaze around a visual barrier (Brauer et al., 2005, Bugnyar et al., 2004, Schloegl et al., 2007).

Another common paradigm to test whether animals understand that gaze cues can refer to objects outside of view is the object-choice task. In this test, animals have to use experimenter-given social cues, such as pointing and gaze, to locate food hidden under one of two containers. Success varies across species; apes often perform inconsistently (Call et al., 2000, Call et al., 1998), African grey parrots rapidly learn to attend to some experimenter cues, but in most cases they did not do so spontaneously (Giret et al., 2009), whereas jackdaws use cues that serve a communicative function in humans (von Bayern and Emery, 2009). Perhaps surprisingly, domesticated species,

such as goats and dogs, have had more success than primates (Hare et al., 2002, Kaminski et al., 2005, Emery and Clayton, 2009) but see, Miklosi and Soproni, 2006).

Tactical Deception

Species that forage in social groups share direct competition over access to resources. Selection is, thus, thought to favour individuals that can mitigate these costs by using social knowledge as a means to employ socially manipulative tactics. Hence, the *social intelligence*, *social brain*, and *Machiavellian intelligence hypotheses*, link the cognitive demands of social living with the evolution of enhanced social skills and increases in brain size (Byrne and Whiten, 1988, Dunbar, 1998, Humphrey, 1976).

Tactical deception (TD) has been used to describe how individuals psychologically manipulate the behaviour of others within a social group (Byrne and Whiten, 1985). Behaviours suggested to represent such psychological manipulations have been reported for numerous primate species, but they are anecdotal in nature and not replicable, so their utility as a source of information on social cognition is questionable (Whiten and Byrne, 1988). Interestingly, however, the number of records of tactical deception correlates significantly with neocortex size in primates (Byrne and Corp, 2004). This relationship remains when group size is accounted for, eliminating concerns that larger groups present more opportunities for deception. Furthermore, this relationship is also consistent with the idea that cognitive problem solving is constrained by neocortex size, supporting the link between the evolution of the neocortex and increased complexity of social living (Byrne and Whiten, 1988, Dunbar, 1998, Humphrey, 1976). However, it is not clear whether such behaviours, if they exist, are unique to primates; comparable studies on other species have not focused on their intelligence in the wild. Studies on birds, for example, far exceed those on primates (certainly in terms of the number of observation hours recorded and the number of species studied), but no field study has yet, to the best of our knowledge,

focused on questions of cognition (social or physical). It is, therefore, less likely that such reports of novel social behaviour would be reported for non-primate species.

This does not mean that we have no comparable data on tactical deception in birds. One potential example is the cache-protection behaviour of food-storing corvids. Strategies such as making false caches (stones, small objects; Clayton et al., 1996, Heinrich, 1999), as well as going through the actions of caching but without depositing any items (Heinrich, 1999) could be classified as examples of tactical deception as defined by Byrne and Whiten (1988). It has been suggested that corvids cache inedible objects in view of conspecifics, to learn about others' pilfering intentions or pilfering techniques. To test this, Bugnyar and colleagues (Bugnyar et al., 2007) allowed ravens to cache plastic objects in front of either a pilfering (P) bird or an onlooker (O) human. After caching, P always stole the ravens' caches, whereas O inspected the objects but never stole them. The ravens were then allowed to cache food; again in front of P or O. Ravens that had experienced the P condition cached food more quickly, hid food behind obstructions, and made more of an effort to conceal their stores than those in the O condition. However, this pattern was not repeated with objects, suggesting that the caching of inedible objects might be used as a deceptive tool to learn about an individual's propensity to steal food (Bugnyar et al., 2007).

Another potential example of tactical deception is moving caches between cache sites in front of an observer (Emery and Clayton, 2008). If jays had cached items in specific locations in front of a specific observer and then retrieved these caches in front of the same or a different observer, they recovered only those items that the observer had seen being cached and left the other unknown caches alone. The caches that were recovered tended to be moved around multiple times and were not necessarily left in the last cache site that the jay made a bill probe into (Dally et al., 2006). This suggests that the caching jays may have been deceiving the observers about the final location of the cache.

Physical Reasoning

It is a long-held assumption that species that employ the use of tools to aid in procuring food from inaccessible areas have greater intelligence, especially in terms of physical cognition, than those species that do not use tools (Emery and Clayton, 2009b). Although chimpanzees use a variety of tools in the wild, there is little evidence that they necessarily understand how the tools that they use work (Povinelli, 2000). Indeed, there is also good evidence that chimpanzees perform better on physical tasks when they do not have to use a tool, compared to versions of the same task requiring tool use (Seed et al., 2009b). There is also substantial evidence that the physical cognition of non-tool-using animals is not fundamentally different to that of tool-using animals (Emery and Clayton, 2009b).

Although there does not appear to be a striking cognitive difference between tool users and non tool-users, there are differences between species. Studies on corvids and apes have found a shared aptitude for folk physics or understanding the functional properties of tools. Using similar test paradigms, corvids and apes both demonstrate the ability to select, modify, and manufacture tools according to the specific demands of a given problem. New Caledonian crows (NCC) and rooks spontaneously select tools of a certain size or length to access concealed food items (NC crows, Chappell and Kacelnik, 2002, 2004, rooks, Bird and Emery, 2009b) as well as manufacture tools with respect to the functional requirements of retrieval tasks (NC crows, Weir et al., 2002, rooks, Bird and Emery, 2009a). Similarly, gorillas and orangutans are capable of selecting tools with properties relevant to specific tasks (Mulcahy et al., 2005).

New Caledonian crows (Taylor et al., 2007, 2010), rooks (Bird and Emery, 2009a), gorillas, and orangutans (Mulcahy et al., 2005) are also capable of sequential tool use (i.e., using a small tool to acquire a larger tool suitable for accessing food). Such tasks are thought to present additional cognitive challenges to that of regular tool use, because they require hierarchical

forethought. Accordingly, the related metatool use or use of one tool to shape another into a better tool (e.g., stone-knapping) represents an important breakthrough in hominid evolution (St Amant and Horton, 2008). Although corvids and great apes rapidly accomplish sequential tool tasks, monkeys have had limited success, often persistently attempting to retrieve a food reward directly with an inadequate tool (Hihara et al., 2003, Santos et al., 2005). Corvids and apes, however, demonstrate an advanced ability to manage their primary inhibitions and organise their behaviours in a hierarchical fashion (Taylor et al., 2007).

Corvids and apes also demonstrate the ability to change the form of one object to manufacture a tool (such as break side twigs off a branch to make a straight stick) or shape and manipulate materials to make them into better tools (such as sculpting the end of a broken-off branch into a hook tool). One apparent difference between corvids and apes is the ability of both NCC and rooks to manipulate a seemingly non-functional (in the context of the experiment) novel material (metal wire) into a new functional tool (a hook), which could then be used to pull up a bucket containing food located in a vertical tube (Bird and Emery, 2009a, Weir et al., 2002). Such behaviours suggest that these two species of corvids understood that, to retrieve the food, they had to (1) pull the bucket upward to remove the food from the well, (2) recognise the inadequacies of the available tool (straight wire instead of a hook), and (3) identify the malleable properties of the wire (which could be fashioned into a hook; Emery, 2006). What is perhaps most striking is that rooks do not use tools in the wild, so they must have formed a mental image of a successful hook tool (which they had used in a previous study and which was completely different in shape and structure to the available materials in the latter task) and modified the novel material into a hook based on this mental image. Rooks (Bird and Emery, 2009b) and orangutans (Mendes et al., 2007) have also demonstrated innovative flexibility when faced with a similar problem based on an Aesop's fable in which food was located inside a vertical tube without a bucket. Both species spontaneously solved the problem. In the case of the rooks, some water was contained inside the tube,

so the rooks dropped stones into the tube to raise the level of the water and thus bring the food into reach. In the case of the orangutans, the tube contained no water, so the apes spat water into the tube, so that the food could float to within reach.

Extractive foraging and tool-using behaviour have thus been considered important mechanisms for driving the evolution of primate intelligence (Byrne, 1996, 2004, van Schaik et al., 1999). Further support is also found in the relationship between relative brain size and the amount of reported tool use in primates (Reader and Laland, 2002) and birds (Lefebvre et al., 2002). However, the sophisticated understanding of the physical properties of tools demonstrated by non-tool-using species, such as rooks (Bird and Emery, 2009a, 2009b), suggests the possibility of a domain-general cognitive toolkit, rather than domain-specific adaptive specialisations that have evolved to solve specific tool-related problems (Bird and Emery, 2009a, Emery and Clayton, 2009b). Such findings question previous accounts that correlate physical intelligence specifically with tool use.

Mental Time Travel

Mental time travel (MTT) is the ability to recall subjective experiences and project oneself into the past or future to re-experience or pre-experience specific events. However, the unique component of such an episodic form of cognition, be it episodic memory or future thinking, in contrast to semantic knowledge, is that its utility invokes individual perspectives that are detached from current mental states (Clayton and Russell, 2009).

Although MTT is a feature of human cognition (Suddendorf and Corballis, 2008), recent work has challenged the view that it is uniquely human (Raby et al., 2007, Raby and Clayton, 2009). To do so, one must develop criteria that tap the behavioural elements of episodic cognition, given that it is impossible to test the phenomenological aspects of re- and pre-experience in the absence of any agreed behavioural markers of consciousness in non-

linguistic animals. Clayton and Dickinson (1998), therefore, suggested that one could test whether an animal could remember the what, where, and when of a specific event, and termed this “episodic-like” memory. Hence descriptions of MTT in nonverbal animals are often referred to as *episodic-like* or *what- where-when* (WWW) memory.

A number of studies have subsequently shown that this form of MTT, or WWW memory, is present in a variety of nonhuman animals, including corvids (Clayton and Dickinson, 1998, Zinkivskay et al., 2009), chickadees (Feeney et al., 2009), apes (Martin-Ordas et al., 2010) and rats (Babb and Crystal, 2006a, 2006b). Subsequently, it has also been found that animals can take action now for the future, suggesting that they also have the prospective component of MTT (for example, Correia et al., 2007, Mulcahy and Call, 2006, Osvath, 2009, Osvath and Osvath, 2008, Raby et al., 2007).

Possibly the most convincing evidence for MTT in nonhuman animals has been documented for corvids and apes. Capitalizing on their natural propensity to cache food, detailed experiments on Western scrub jays have revealed that they understand what items of food they stored, where they stored them, and when these items were stored (Clayton and Dickinson, 1998). Clayton and Dickinson (1998) presented jays with the opportunity to cache perishable wax worms and nonperishable peanuts. Following caching, the jays were subjected to two experimental conditions of either a short delay prior to retrieval (4 hrs) or a long delay (124 hrs). After a short delay, jays preferentially searched for wax worms, which were favoured over peanuts. However, after experiencing a long delay, in which the worms had decayed and become inedible, jays avoided searching for the worms and instead recovered peanuts. The preferential recovery of particular food items, depending on when they were cached, suggests that the jays used an episodic-like memory to recall past experiences about the degradation rates of different food types, as well as where and when each item of food was stored.

Further experiments have revealed that jays' caching decisions are constructed from anticipating their future needs, irrespective of their current motivational states (Correia et al., 2007, Raby et al., 2007). Raby and colleagues (2007) housed jays in one of two separate rooms over six alternate days. In one room, they were always given breakfast and in the other they were not. After this training period, the jays were unexpectedly given food to eat and cache in the evening. Raby and colleagues (2007) found that the jays stored more food in the non-breakfast room, where they could expect to be hungry the following morning, compared to the room where breakfast was provided. In a second "breakfast-choice" experiment, Raby and colleagues (2007) controlled for any conditioning that may have influenced caching in places associated with hunger by always providing breakfast in each room. However, in this experiment, each room was associated with a particular type of food (i.e., dog kibble or peanuts). If the jays based their caching decisions on a conditioned response, formed from associating a particular room with a particular food, they would be predicted to cache dog kibble in the room previously associated with dog kibble and vice versa. However, jays in this experiment cached more of the different food rather than the same food in each room, suggesting that they preferred a choice of food at breakfast and were capable of forward planning (Raby et al., 2007).

Using a similar methodology to Clayton and Dickinson (1998), but with preferred perishable (because it was frozen and could melt) juice and less preferred, but nonperishable grapes, Martin-Ordas and colleagues (2010) recently found that chimpanzees, orangutans and bonobos were capable of distinguishing between different events in which the same food items were hidden in different places at different times, suggesting that the apes also remembered in an integrated fashion what, where and when certain events occurred (Martin-Ordas et al., 2010).

Likewise, Mulcahy and Call (2006), found that apes are capable of selecting, transporting, and saving a suitable tool, not because they currently needed it,

but because they would need it in the future. Apes learned to use a tool to obtain a reward from an apparatus. In a separate testing room with no apparatus, the apes were then provided with a choice of one out of two suitable and six unsuitable tools. The subjects then experienced either a 1- or 14-hour delay after which they were allowed to return to the test room, with their selected tool, to access the apparatus. The apes succeeded in selecting and retaining appropriate tools for future use (Mulcahy and Call, 2006). Similar results were also found in studies that increased the cognitive load of subjects by disassociating the locations of the tool and apparatus as well as increasing the delay period and housing subjects socially instead of individually (Osvath and Osvath, 2008).

WELCOME TO THE CLEVER CLUB

Although we have primarily restricted our arguments to corvids and apes, we have included examples from other animals where appropriate. Indeed, there is good evidence that cetaceans (whales and dolphins) also demonstrate convergent evolution of cognition with apes (Marino, 2002). We could extend the invitation to parrots; possibly other groups of birds with relatively large brains, behavioural flexibility, and a complex diet, such as hornbills and some birds of prey; elephants; and pack-hunting carnivores, such as hyenas (see Emery, 2006). We would not extend the invitation to domestic dogs because their cognitive abilities, impressive as they are (Miklosi, 2007) cannot be an example of convergence, because their cognitive evolution is likely the result of domestication by humans, rather than a response to socio-ecological selection pressures in their adaptive environment. Domestication thus seems to be the most appropriate hypothesis to explain dogs' intelligence, especially in the social realm.

If our hypothesis is correct, that shared cognitive traits have arisen in distantly related groups such as corvids and apes because they have solved similar environmental problems, then we should expect groups that have faced similar problems to have evolved similar solutions to these problems. This

could be in the form of complex behavioural strategies or cognitive processes. Based on a simple analysis of such problems and similar life-history traits, Emery (2006) found that many animal groups displayed similar traits at the biological, ecological, behavioural and psychological levels (Figure 1.4). Underlying all of these similarities is behavioural flexibility as applied to the solution of problems faced by living in an unpredictable environment (Sterleny, 2003). As such, those species with a varied, ephemeral, and even unpredictable diet, that lived in a complex (but not necessarily large) society, that had a relatively large brain, went through a long developmental period, lived a long life, and lived in a fluctuating habitat, could all be considered candidates for convergent evolution.

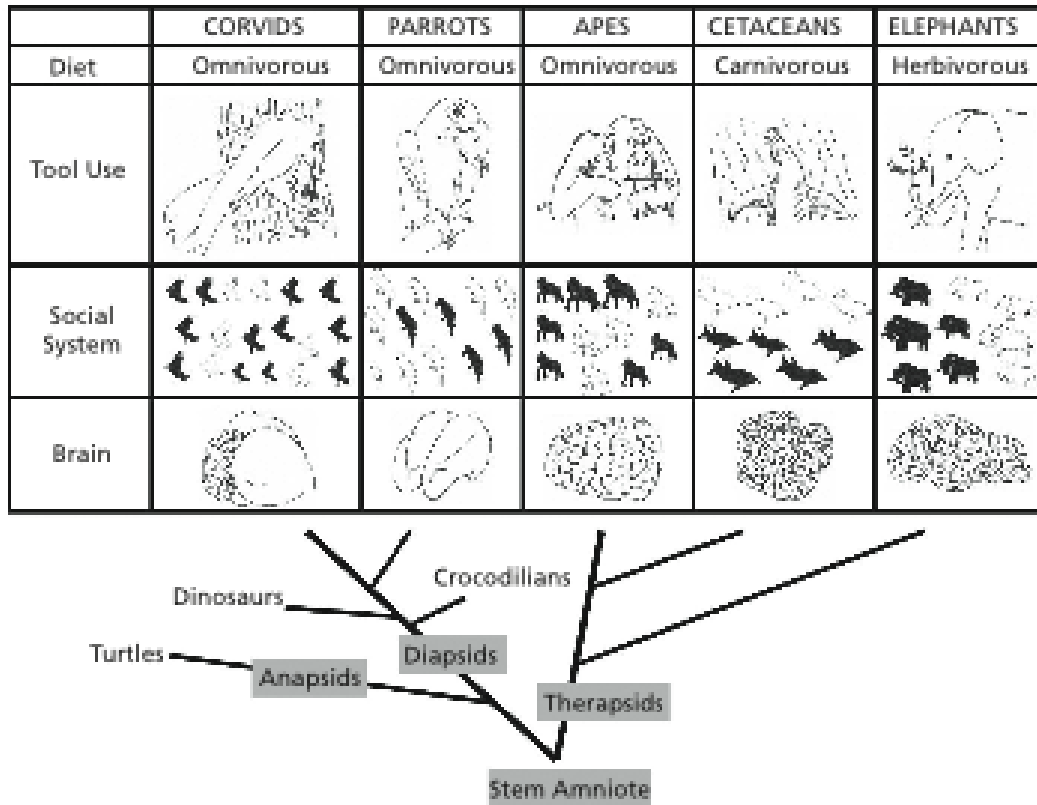


Figure 1.4: Upper. Diagram displaying various biological (brain structure), ecological (diet), and behavioural (tool use [stick use by New Caledonian crows, wood-tool aid to opening palm nuts in hyacinth macaws, termite fishing in chimpanzees, sponge-tool use by dolphins, fly switching by elephants]), and social-system (black and white figures represent different individuals within a social group and so the variety of individuals suggest social complexity) traits in corvids, parrots, apes, cetaceans, and elephants. Despite very different brain structures, such as the lack of cortical folding in birds but extensive folding in apes, cetaceans, and elephants, there are striking similarities in the diet, use of tools, and social system, in these distantly related animal groups. Lower. Basic evolutionary tree displaying the relationships between these main animal groups.

CONCLUSION

It is likely that there is no one particular mechanism that is responsible for driving the evolution of cognition across all species. Cognition is, instead, likely to have evolved as a result of the many challenges animals face in their environments. Group living may have provided a foundation for social cognition and, hence, social cooperation and manipulation, but qualitative

relationships in the form of monogamous pair bonds or the arms race between cachers and pilferers may have also been important. Similarly, methods for manipulating the environment, such as building a nest or extractive foraging (with or without tool use) may have provided the foundation for physical cognition. Although still not clear, it seems probable that neither the social or physical realm alone drove the evolution of intelligence. Rather, the ability to adapt to a changing environment, as encountered by the species under consideration here, is perhaps the best explanation we have for why some animals display the cognitive abilities they do and why such abilities have evolved convergently in very distantly related groups.

1.4: A Review and Analysis of Parrot Cognition

Most people consider parrots intelligent animals; after all they are often prized as family pets for their communication skills and endearing behaviour. However, surprisingly little is known about the cognitive abilities of parrots. In a search of academic publications on the topics 'Primates' and 'Cognition' in early August 2013 on the ISI Web of Knowledge, 30,301 results were identified. Yet when replacing 'Primates' with 'Parrots' only 113 results were found (Figure 1.5). Furthermore, of those 'Parrots' results, an overwhelming proportion of the research focused on only one species; African greys (*Psittacus erithacus*) by Irene Pepperberg. Of course, with further probing into the literature additional studies can be found, however the point remains that cognitive research, and hence our understanding of animal cognition remains predominantly primate-focused. From an anthropocentric point of view, an approach that focuses on species that are morphologically, socially and genetically similar to humans would appear justified. However, clues to the convergent evolution of cognition through similarities in socio-ecology can only be found by looking at a wider range of more distantly related species. This review will highlight and discuss recent research on the cognitive abilities of parrots and suggest that further investigation of this group is likely to yield promising breakthroughs in the field of comparative cognition and thus our understanding of the evolution of cognition. As such, it will introduce the areas of research investigated in this thesis.

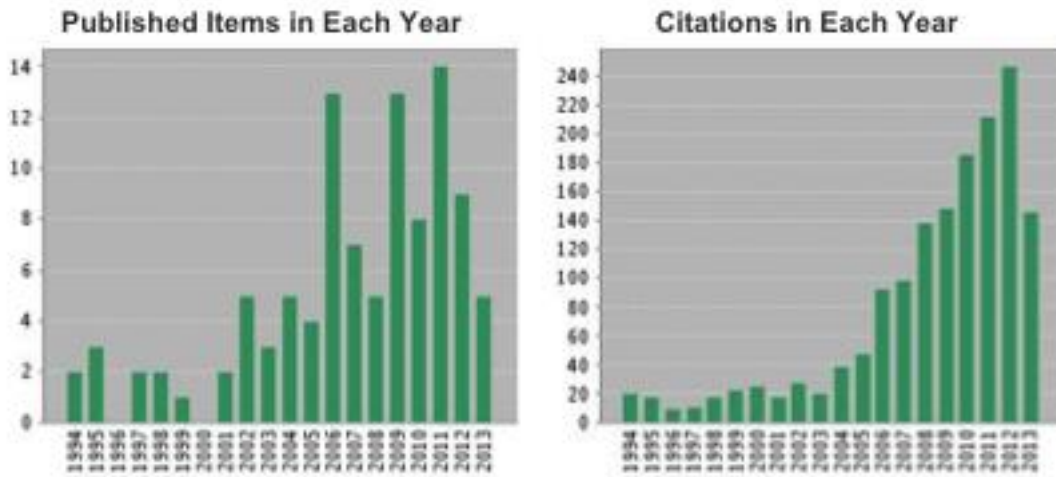


Figure 1.5: The number of publications and citations of papers across the last 20 years (1994-2013), as revealed from an ISI Web of Knowledge search on 'Parrot Cognition' in August 2013. Comparable figures for a search on 'Primate Cognition' was not available as the search contained more than 10,000 records.

Concepts, Number & Language; with a focus on African greys

Irene Pepperberg's research on Alex, the African grey parrot, has made a substantial contribution to the literature on parrot cognition over the last three decades (Pepperberg, 1999). Throughout this period, Alex received considerable training on referential English labels and was habituated to a variety of cognitive tasks. As a result, Alex revealed cognitive abilities that rivalled those of nonhuman primates, marine mammals and young children up to the age of four (Pepperberg, 2006a). Alex showed a competent understanding of numerosity and could use English labels to add up to six novel items, including random patterns and subsets of mixed groups (e.g. number of blue blocks within blue and green blocks and balls; Pepperberg, 1994). What's more, Alex's accuracy was unaffected by quantity, mass or contour (Pepperberg, 1994), and he also showed a spontaneous and untrained understanding of 'none', or a 'zero-like concept' with respect to the absence of items (Pepperberg, 2006b, Pepperberg and Gordon, 2005). An understanding of such abstract concepts is interesting as 'zero' or 'none' lack a concrete reality; yet still represent information through the absence of

objects. Such abilities require cognitively complex mental representations of objects and can confuse children under 4 years old (Bialystok and Codd, 2000).

Some non-human animals can sum small quantities, generally less than four (Pepperberg, 2006a, Boysen and Berntson, 1989, but see Hunt et al., 2008), while others are sensitive to ordinality, numerosity, number concept, and mass if not number (see Pepperberg and Gordon, 2005 for a more detailed review). Several researchers have thus considered advanced numerical abilities (counting of quantities of 4 or more) to be uniquely human and based on language skills (Spelke and Tsivkin, 2001). Pepperberg's studies however are the first to report advanced numerosity in a non-human, non-primate, non-mammalian subject (Pepperberg, 2006b); with results comparable to the summation capacities of chimpanzees and children (Pepperberg, 2006a). Such pioneering research helped dissolve indoctrinated views that the great apes, including humans, are unique in their possession of complex cognition.

Renowned for their intellect, African greys have also received attention from other research groups. Greys have demonstrated the ability to spontaneously categorise items according to their perceptual similarities using referential French and Czech labels (Giret et al., 2009c) and can possibly discriminate between conspecifics visually and acoustically (Giret et al., 2009b). Moreover, these birds have been tested on numerous tasks that have been performed on a variety of other species, suggesting that they possess similar cognitive capacities. When presented with varying amounts of food, African greys (Al Ain et al., 2009) like great apes (Hanus and Call, 2007), can discriminate between large and small quantities. Although African greys, unlike primates, show difficulty in performing delay gratification tasks (Vick et al., 2010), Goffin cockatoos have recently demonstrated an ability to inhibit the retrieval of a desirable food item for larger or better quality rewards (Auersperg et al., 2013). One African grey has also demonstrated the ability to spontaneously use proximate experimenter pointing gestures to locate food items, while two others learned to respond to this cue after 15 trials. However, none of the

subjects spontaneously responded to experimenter eye-gaze cues. Although again, one subject rapidly learned after 15 trials (Giret et al., 2009a). Similar results have been found in other species; non-human primates (Tomasello et al., 1998), goats (Kaminski et al., 2005), dogs (Viranyi et al., 2008) and corvids (von Bayern and Emery, 2009).

Many of these studies have revealed that African greys possess similar cognitive abilities to those of other large brained species, such as corvids and apes. However, interpretations of such results are often based on the performances of only one, if not a few individuals. A low sample size may be due to the limited availability of birds, as well as the considerable amount of time and funds required to maintain such species. While these findings reveal that certain species are capable of sophisticated cognition, such results may only include individuals that are particularly motivated to engage in experiments or with an experimenter. Hence, it may be difficult to replicate such findings, or interpret results to make broad species-wide generalisation.

Apart from African greys, the only other species of parrot that has received considerable cognitive investigation is the New Zealand kea. Renowned for its extreme neophilia and curious yet destructive behaviour (Diamond and Bond, 1999), the kea is considered a prime candidate for advanced cognitive capabilities (Schloegl et al., 2009) and has thus been the recent focus of many cognitive studies (Huber and Gajdon, 2006).

Technical Intelligence & Social Learning

Piaget and cognitive development

Human cognitive research has focused on common processes associated with skill development in infants (Piaget, 1953, 1954). Such developments include a subject's initial understanding about interactions with their physical surroundings to a more complex insight into problem-solving and intellectual representation (see Uzgiris and Hunt, 1989). The Piagetian framework was

later adopted as a relevant method for testing comparative cognitive development across species and applied to our closely related ancestors the non-human great apes (Redshaw, 1978, Mathieu et al., 1980, Poti and Spinozzi, 1994) and other non-human primates (c.f. Tomasello and Call, 1997). However, researchers have only recently used the Piagetian framework as a comparative approach to assess the convergent evolution of cognition amongst more evolutionarily disparate species (Auersperg et al., in press, Funk, 2002, 1996a, 1996b, Pepperberg, 2002b, Pepperberg and Funk, 1990, Salwiczek et al., 2009, Zucca et al., 2007).

Funk (1996a, 1996b) first used the Piagetian framework to test skill development in parrots (indeed the first to examine non-primates) by comparing the convergent features of early cognitive development in human infants with those of kakariki (*Cyanoramphus auriceps*). Notably, Funk (2002) adapted a battery of tasks designed for use on human infants (see Uzgiris and Hunt, 1989) to assess development of means-end problem solving skills in kakariki (i.e. means for obtaining desired events). This test battery documented the order of developing certain behaviours such as: attaining and playing with objects, retrieving rewards through the use of a stick or rake and pulling rewards attached to the ends of strings. While Funk (2002) revealed similarities between the cognitive development of human infants and birds on such tasks, the order in which kakariki completed certain tasks differed from those of human infants. The ability to use locomotion to obtain objects developed earlier in Funk's parakeets than in human infants. Moreover, unlike human infants, there was variation in the order in which a series of means-end pulling tasks were solved. Young kakariki also did not place items inside a container or stack objects on top of each other as observed in infants and non-human primates (Funk, 2002).

Although similar means-end tasks, such as string-pulling (Figure 1.6), had previously been presented to a variety of bird species, such as budgerigars (*Melopsittacus undulates*), Indian starlings (*Acridotheres tristis*) and jackdaws (*Coloeus monedula*) (Ducker and Rensch, 1977), Funk's experiments (2002)

prompted a series of further investigations establishing string-pulling as a comparative hallmark of cognitive behaviour across a number of distantly related species (for a more in-depth review of string pulling in birds see Chapter 5).

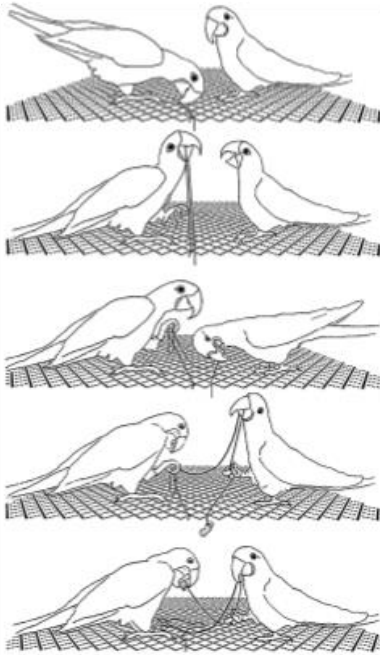


Figure 1.6: Example of a typical sequence of acts employed by hyacinth macaws during a string-pulling task (drawing by Wladimir J. Alonso); from Schuck-Paim and colleagues (2009).

String-pulling and means-end tasks

Parrots have received long-standing recognition for possessing attributes that are characteristic of a folk intelligence (Boehrer, 2004, Carter, 2006). Although there are over 350 species of parrots (Juniper and Parr, 2003), and they are generally considered to possess advanced cognitive capacities (Emery, 2006), our understanding of parrot cognition is still limited to a few species (Schuck-Paim et al., 2009). Of those species investigated, string-pulling behaviour has become a common method for assessing and comparing cognitive capacities. Most parrots tested on this paradigm efficiently solve simple food-retrieval tasks without training on their first trial (Schuck-Paim et al., 2009, Werdenich and Huber, 2006, Magat and Brown, 2009, Pepperberg, 2004, Krasheninnikova et al., 2013, Krasheninnikova and

Wanker, 2010), if not after a few trials (Funk, 2002). Of those parrots tested, kea, *Nestor notabilis*, (Werdenich and Huber, 2006), African greys, *Psittacus erithacus*, (Pepperberg, 2004), three Neotropical species; hyacinth macaws (*Anodorhynchus hiacynthinus*), Lear's macaws (*Anodorhynchus leari*) and blue-fronted Amazons, *Amazona aestiva*, (Schuck-Paim et al., 2009) as well as spectacled parrotlets, *Forpus conspicillatus*, (Krasheninnikova et al., 2013) appear to show the most convincing evidence of a causal understanding of means-end problem solving; initially adopting their most efficient method of retrieval and showing no further improvement in performance throughout subsequent trials.

Overall, string-pulling results suggest that parrots can discriminate between strings baited with rewards and those without (Funk, 2002, Krasheninnikova et al., 2013, Pepperberg, 2004, Schuck-Paim et al., 2009, Werdenich and Huber, 2006), with some macaws capable of determining connectedness through physical continuity i.e. no gaps in string (Krasheninnikova et al., 2013, Schuck-Paim et al., 2009). However, most parrots fail to recognise the functional connection between crossed rewarded and non-rewarded strings. Even when different colours were used to help visually track the course of the reward, parrots generally have difficulty succeeding in this task (Krasheninnikova et al., 2013, Schuck-Paim et al., 2009). Although Werdenich and Huber's kea (2006) performed extremely well on the discrimination tasks, only one kea out of seven chose the correct crossed string in the first 30 trials. Three birds learned quickly after failure in the first trial, one bird after a number of failures and two birds remained at chance. However, after an additional 30 trials, all birds' choices were overwhelmingly correct (91%). Yet, when provided with the same colour strings, on subsequent trials, only three birds performed above chance (Werdenich and Huber, 2006).

The ability to solve string-pulling tasks may also be influenced by differences between species' life histories. In a recent study that compared eight different species of Australian parrots, Magat and Brown (2009) found that only those

parrots that used their feet while foraging were capable of solving the string-pulling problem. In addition, strongly lateralised parrots (i.e. species that preferentially process information in one hemisphere of the brain) also solved string-pulling problems more successfully than non-lateralised parrots. Species that use their feet while foraging may possess more advanced motor coordination than those that do not, thus enabling them to more readily solve such tasks. Differences in foraging methods are also likely to promote different anatomical specialisations in parrots. As such, a necessity to manipulate objects while foraging may correspond with differences in dexterity and visual acuity (Demery et al., 2011). The question then remains whether causal reasoning corresponds with motor flexibility or whether comparisons of species that possess different capabilities on tasks that require such coordination provide ecologically valid results.

In another experiment, two African greys with considerable training in referential English in Pepperberg's experiments (2004) made no attempt to retrieve the reward but instead attempted to manipulate their trainer by making verbal requests for the reward. Conversely, two African greys with limited vocabularies immediately performed the correct physical actions to obtain the reward. Engaging in communication as a problem solving strategy may thus suggest that a more advanced stage of cognitive development can be acquired through enculturation. Those species of parrots with capacities to learn human language are also likely to possess an advantage over other species that lack such abilities. Enculturation may also facilitate cognitive development and thus explain why hand-raised birds often outperform wild birds on cognitive tasks (Gajdon et al., 2004, Gajdon et al., 2006, Funk, 2002, Pepperberg, 2002b). Such effects are further discussed below.

Although string-pulling discrimination tasks are often successful, researchers frequently observe the retrieval of strings with no rewards attached, suggesting that string pulling itself may be a self-rewarding process (Pepperberg, 2004, Schuck-Paim et al., 2009). It is thus difficult to disentangle whether subjects demonstrate a causal understanding of why and

how their actions cause certain effects. In addition, it is difficult to infer causal reasoning when solutions to string-pulling tasks are provided by tangible cues in the experimental design (i.e. connectivity and weight).

Another method used to assess Means-End causal reasoning, which addresses some of the aforementioned limitations of the string-pulling paradigm, is the Physical Support problem (Auersperg et al., 2009, Hauser et al., 1999, Piaget, 1953). In this test, subjects are presented with two horizontal supports (spatulas), one with a reward resting on the top and the other with the reward resting next to it. If the subject chooses the correct 'connected' spatula i.e. that with the reward placed on top, the subject will be able to retrieve the reward and thus causal reasoning is inferred (see Chapter 5). Hence, subjects must make decisions based on visual cues alone, without experiencing external cues, such as differences in weight for example. Auersperg and colleagues (2009) found that one of six kea showed a spontaneous comprehension of means-end relationships by selecting the correct spatula based on the connections between supports and rewards. Such results rival those found in other species on similar Support Problems, such as cotton-topped tamarins (Hauser et al., 1999), chimpanzees (Spinozzi and Poti, 1993) and a blue-fronted Amazon (de Mendonca-Furtado and Ottoni, 2008). The poor performance but eventual success of the blue-fronted Amazon in de Mendonca-Furtado and Ottoni's (2008) study suggests the possibility that their subject alternatively memorised the connected-reward solutions, rather than showing a causal understanding of the problem.

Another popular paradigm to test causal reasoning is the Trap-Tube task (Seed et al., 2006, Seed et al., 2009b). This task is similarly designed to assess whether non-tool-using corvids and apes can comprehend the outcome of their actions. To solve this task, subjects are required to attend to the functional and non-functional differences between trapping holes. Success on this task is therefore considered to indicate a causal understanding of the functional properties of traps. However, while results from this paradigm provide some evidence that rooks understand the causal

principles underlying this task (Seed et al., 2006), kea, red-and-green macaws (*Ara chloroptera*) and sulphur-crested cockatoos (*Cacatua sulphurea*) failed to succeed (Liedtke et al., 2010)

Exclusion

Exclusion Performance tasks are another Piagetian method used to assess causal reasoning between species. In this test, for example, subjects are provided with a choice between two cups that potentially contain concealed rewards. However, unbeknown to the subject, only one cup is rewarded. Prior to choosing, the subject is then informed that one of the cups does not contain a reward. The contents of the baited cup, or the un-baited cup may be revealed. Subject's are then considered to possess a causal understanding of the task if they can infer the correct option via an 'exclusion- driven' decision.

Schloegl and colleagues (2009) presented kea and ravens (*Corvus corax*) with a choice task that required subjects to search for food in either straight or bent tubes. When provided with partial information about the content of one of the tubes, kea inferred the location of hidden food by choosing the baited tube more often than ravens. However, ravens applied a more efficient strategy i.e. their first look was usually sufficient to make their choice and, in contrast to the kea, ravens looked into both sides of the tubes infrequently. It is thus thought that ravens made their decisions based on exclusion, whereas the kea showed more exploratory behaviour, by making redundant search efforts i.e. looking into both sides of a straight tube, did not understand the causality of the task. Such differences may be attributed to peculiarities in each species' natural history and thus provide insight to the adaptive pressures that drive the evolution of certain cognitive processes. For example, one explanation to account for the more efficient behaviour of ravens in the above study is that ravens typically forage in a more competitive environment than kea (Schloegl et al., 2009). Conversely, kea are highly neophilic extractive foragers and are often required to explore their environment to gain access to unreliable resources. Hence, both behaviours

may be adaptive within their respective environmental contexts. As a result, selection pressures that favour foraging efficiency may influence the evolution of cognition, yet ecologically valid interpretations of such behaviours are necessary.

More recently, parrots have demonstrated performances on more complicated inferential reasoning tasks that have only previously been demonstrated in chimpanzees and children (Premack and Premack, 1994). Mikolasch and colleagues (2011) visibly baited two cups with two different rewards. An experimenter then secretly removed one food type and showed it to the subject. After receiving such information, one in seven African greys successfully selected the baited cup (Mikolasch et al., 2011). Pepperberg (in press) successfully replicated these findings, with three of four African greys solving the problem. Furthermore, Schloegl and colleagues (2012) found that African greys could successfully solve similar inference tasks based on auditory cues. However, surprisingly, parrots were only successful when the containers were shaken horizontally, but vertically (Schloegl et al., 2012). Spontaneous success on this task had only previously been demonstrated in apes, which were also capable of using the absence of noise to infer the location of the reward (Call, 2004).

Tool-use in parrots

Many animals use tools to extend their physical influence on their surrounding world. However, tool-use requires dexterity and a certain understanding of cause and effect or means-end reasoning. Hence, tool-use has been considered a useful correlate of intelligence (Lefebvre et al., 2002). Although many parrots manipulate food with their feet and are extractive foragers, surprisingly few observations of tool-use have been documented. Most notably, Borsari and Ottoni (2005) observed captive hyacinth macaws (*Anodorhynchus hyacinthinus*) using tools, wedge-like pieces of wood, which were positioned beneath the birds' upper mandible and used to more efficiently grip nuts. Whilst holding the nut in place with the foot, birds then

opened the hard casing with their lower mandible. Similar behaviours have also been observed in the black palm cockatoo (*Probosciger aterrimus*) by Wallace (2000) in 1869.

While parrots may not regularly be challenged with a necessity to use tools in their natural environment, captive species of parrots show convincing capacities for tool related behaviours. Captive kea have been reported to show tool-using behaviours that are comparable to those of regular tool using New Caledonian crows (Auersperg et al., 2011). Moreover, a captive Goffin's cockatoo (*Cacatua goffini*) was recently observed to spontaneously employ a number of techniques and materials to successfully manufacture stick tools to retrieve otherwise out-of-reach cashew nuts (Auersperg et al., 2012). These observations suggest that parrots possess sophisticated tool-related behaviours, yet the paucity of such accounts may also suggest that these species do not need to regularly use tools because they possess dexterous feet and a multipurpose bill (for a more in-depth review of tool-use see Chapter 5).

Social learning, attention and emulation

Extractive foragers are often faced with the difficult task of manipulating food items for consumption. Techniques can often take years to perfect, resulting in variable success rates within a group. For example, wild bearded capuchins (*Cebus libidinosus*) crack palm nuts, yet individual success rates vary from 6.6-75 strikes per nut (Fragaszy et al., 2010). As such, learning the affordances of tasks by observing skilled conspecifics may enhance the performance of inexperienced individuals. However, a novice still requires an ability to understand the causal relationships of extractive processes such as connectivity or the construction of a chain of responses that lead to a goal.

The spread of innovative behaviour through observational learning is a useful tool when comparing and assessing social cognition between species (kea: Gajdon et al., 2004, 2006, kea, dogs and children: Range et al., 2009). Huber

and colleagues (2001), for example, found that captive kea opened a complex food container more efficiently after observing a skilled conspecific successfully perform the task. This study suggests that kea learnt something about the functionality of the container and the actions of the demonstrator during observation, suggesting that they were attentive to possess of social learning. Heyes and Saggerson (2002) have also shown that observer budgerigars adopt the same behaviour as demonstrators through motor imitation.

However, behaviours revealed among captive populations may not necessarily reflect those observed in the wild. Wild and captive animals are often confronted by different socio-ecological challenges. For example, wild animals might spend more time foraging and defending territories from rival groups, whereas captive animals may interact more with their peers or humans, showing little concern for the availability of food. Through extensive exposure to humans and human paraphernalia, captive animals might also become less neophobic and more habituated than wild animals (van de Waal and Bshary, 2010). Indeed, Gajdon and colleagues (2004) found that captive kea outperformed wild kea in a social learning task that required subjects to remove a tube from an upright pole to retrieve a reward. When presented with novel foraging problems, captive kea may therefore experience disproportionately high levels of social information in contrast to wild kea, possibly because captive individuals are confined within a limited area. Wild kea, by comparison, may rarely encounter such abundant, clumped resources in their natural alpine environments. Hence, the transmission of foraging innovations observed among individual wild kea, such as the opening of rubbish-bin lids, does not readily spread through a population (Gajdon et al., 2006). Importantly, both studies confirm that wild and captive birds were equally motivated to solve each task, suggesting differences in social attention and social learning between captive and wild populations.

Conclusion

There are many reasons why parrots are not well represented in comparative cognition literature, despite their reputation for intelligence and their popularity as pets. One is that until very recently, primates were the focus on studies of cognition because of their close evolutionary relatedness to humans and studies of birds, with the possible exception of pigeons, were uncommon. This has now changed with studies on corvids and with a modern understanding of the organisation of the avian brain and its analogous structures to those of mammalian brains (Emery and Clayton, 2004a, 2005). Another is that despite their popularity as pets, few long-term laboratory studies have been performed on parrots; probably because of their difficulty and expense, but also because parrots can be extremely long-lived. Alex, an African grey, for example, lived to 31 years in captivity, while some of the larger macaws may live up to 100 years in captivity (Brouwer et al., 2000). Parrots also form strong pair-bonded relationships with specific individuals (Forshaw, 1989, Juniper and Parr, 2003), which is likely to make working with a group of researchers complicated. Finally, very little is known about the natural behaviour of parrots because of difficulties in studying them in the wild. Many species of parrots live in closed canopy tropical forests. Parrots may also be well camouflaged and can fly long distances, making it difficult for researchers to monitor their behaviours. As such, comparatively little information is known about the socio-ecology of parrots, which makes studying their cognition and the relationships between their natural behaviour, ecology and cognition, fraught with problems. One possible method for increasing the study of parrot cognition may be to follow the example of recent domestic dog research and test those species of parrots that are available as pets or test captive parrots that are housed in zoos or bird parks.

Despite these issues, parrots share many of the biological, ecological and sociological traits that are thought responsible for advanced cognition in primates. Although our current understanding of parrot cognition is limited to only a few species, predominantly African greys and kea, researchers have

recently recognised that parrots possess similar cognitive capacities to other large brained animals such as corvids and the great apes (Auersperg et al., 2009, 2011, 2012, Pepperberg, 1999). As a result, there is much potential for advancing our understanding of both the physical and social domains of parrot cognition. In addition, further investigation into the cognitive capacities of more distantly related species may illuminate ecologically relevant drivers of cognition that are not so easily identified by studying closely related species such as the great apes.

1.5: General Methods

1.5.1: Subjects and Housing

Four red-shouldered macaws (*Diopsittaca nobilis*): No.2, No.4, No.5, No.8, and four black-headed caiques (*Pionites melanocephala*): Green, Gold, Purple, Red, participated in this study (hereafter macaws and caiques). All subjects were male, with the exception of one female macaw (No.4). Subjects hatched between June and July 2010, were hand-reared and introduced to the lab in September 2010 at three months old. Subjects were identifiable by colour-coded leg bands, and housed according to species in large indoor aviaries (2m³). Each aviary was enriched with rope swings and a variety of branches, perches and toys, which were frequently changed. Subjects were regularly allowed out of their enclosures to fly freely within the lab, although they remained in their respective cages during testing and evenings. Both species were raised under identical conditions and provided with equal experiences. Subjects were kept on a 12:12 h light:dark cycle, with abundant natural light, and maintained on a diet of ad libitum dried fruit and nuts, mixed seeds, and fresh fruit. Food and water were provided *ad libitum* and subjects' participation in experiments was voluntary.

Subjects were selected to participate in these experiments, as they were of a suitable size to house in captivity and readily available from registered breeders in the UK. These particular species were also chosen based on anecdotal reports from breeders and pet owners that suggest characteristics ideal for investigating questions relating to social and physical cognition. These species were also chosen, as their cognitive capacities had not previously assessed.

1.5.2: Ethical Approval

All research undertaken was non-invasive and therefore fell outside of the Animal (Scientific Procedures) Act, and hence did not require Home Office UK approval. Subjects were however housed in accordance with these regulations and the local ethical committee were consulted and agreed to all aspects of this research. Home Office Inspectors and veterinarians regularly visited the lab to ensure these procedures were maintained.

1.5.3: Natural History

For a more detailed description of each species see Juniper and Parr (2003), Schulenberg and colleagues (2007) and Forshaw (1989).

Habitat

Macaws and caiques inhabit overlapping regions in northern Neotropical regions of South America, but occupy contrasting habitats. Red-shouldered macaws are found in stable, open wooded habitats and savannahs, with scattered bushes and various palm groves, and avoid large tracts of closed-canopy forest. Black-headed caiques prefer more heterogeneous, and hence potentially more complex habitats comprised of closed canopy forest and forest edges (Juniper and Parr, 2003).

Morphology

Macaws are slightly larger (30cm) than caiques (23cm), and have longer tail and primary flight feathers. Caiques are much stouter in appearance and are relatively poor long-distance fliers. Macaws, in contrast to caiques, also have much larger down-curved beaks, enabling them to open hard-cased nuts; suggesting that their foraging behaviours may be more specialised than caiques. Both species, however, possess a similar relative brain size

(macaws: brain 5.84ml, body 136g; caiques: brain 5.18ml, body 136.4g); which is comparable to corvids and other parrots (Iwaniuk et al., 2005).

Sociality

Although little is known about the precise social dynamics of these species, parrots generally form long-term pair bonds, roost communally outside of the breeding season and forage in extended family or small social groups (Juniper and Parr, 2003). Both species form pairs in the breeding season, however there is some indication that macaws form larger flocks outside of the breeding season whereas caiques form smaller groups of around 10-30 individuals (Juniper and Parr, 2003).

1.5.4: General Statistical Procedures

Throughout this thesis I have attempted to keep planned, post-hoc comparisons of independent or uncorrelated information to a minimum (i.e. no more than the df of groups). However, in some cases multiple, planned or unplanned comparisons were necessary, given that little preliminary information is available for these species to form hypothesis driven questions. On such occasions I present data where I have not corrected α (0.05) for multiple post-hoc tests (reported as an “uncorrected” test). When multiple tests or comparisons are conducted (i.e. post-hoc t-tests after a significant ANOVA), the probability of at least one Type I error among a family of tests increases (i.e., rejecting H_0 , the null hypothesis, when H_0 is true). For example, in 3 tests the family-wise probability of at least one Type I error is 0.14, at 19 tests its 0.40, at 45 tests its 0.90 (Quinn and Keough, 2010p. 49). Bonferroni corrections may therefore be used to control for Type I errors. To do this, the nominated significance level, α (0.05), is divided by the number of comparisons in the family. However, a problem associated with this procedure is that multiple comparisons become increasingly conservative and suffer from low statistical power (Quinn and Keough, 2010 p. 49). There is however some evidence in favor of not adjusting significance levels, at least

for multiple planned comparisons, particularly for sample sizes of less than 30 individuals (Nakagawa, 2004). Quinn and Keough (2010p. 197) provide the following advice “our broad recommendation is that the default position should be no adjustment for multiple testing if the tests represent clearly defined and separate hypotheses”; with the following conditions “... that the number of comparisons is small so that the increase in family-wise Type I error rate will also be small and each comparison is of specific interest so power considerations are particularly important.”

Multiple unplanned comparisons, which do not represent clearly defined and separate hypotheses, may however, warrant some control over Type I error rates. A preferred method, over that of Bonferroni corrections, is Tukey’s HSD test. While I report Tukey’s post-hoc tests following a significant ANOVA when planned comparisons between more than two groups were required (i.e. Chapter 3; 3.1), such tests are not generated in SPSS (SPSS for Mac OS X, 2007) when making between-species comparisons of only two groups. Hence, due to the limitations outlined above, I report uncorrected post-hoc tests for multiple unplanned between-species comparisons, rather than adjusting α according to Bonferroni corrections. However, as all unplanned comparisons in this thesis report non-significant findings, this approach may be justified because any post-hoc Bonferroni corrections would not change any interpretations of the results.

Chapter 2: Behavioural Observations

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2.0.1 Abstract

Behavioural observations of macaws and caiques were undertaken when subjects were 4 months old and again when subjects were 24 months old. At four months old, instantaneous scan-sampling procedures were used to assess between-species propensities for social interactions, such as play and preening behaviours, and preferred social clique size. Foraging behaviours and inedible object manipulation were also assessed for each species during this period. At 24 months old, the structures of social relationships were quantified using continuous focal-sampling procedures. Agonistic interactions between individuals were used to calculate David's scores and determine dominance ranks for individuals of each species. Affiliative interactions between dyads were also used to determine the strength of pair-bonded relationships. At four months old, pronounced between-species differences in social behaviours were observed. Caiques engaged in social play more frequently than macaws. Macaws, however, participated in social preening more often than caiques. There were no between-species differences in frequencies of inedible object manipulation. Macaws were generally observed in larger social units, whereas caiques often remained solitary. Few between-species differences in foraging behaviours were observed. At 24 months, agonistic interactions revealed a clear linear dominance hierarchy within each species. Affiliative interactions also revealed some directionality, suggesting that the strength of pair-bonded relationships differed between individuals. While affiliative relationships appeared to have stabilised between the two sampling periods (i.e. as the birds matured into adults), macaws spent a greater amount of time engaging in affiliative behaviours than caiques. Overall, these findings reveal differences in the social behaviours of macaws and caiques. Although macaws may be particularly social in comparison to caiques, such relationships may also be developed and maintained through different types of affiliative interactions. Such results, however, need to be interpreted with a significant degree of caution as they are based on very small sample sizes that were available for each species.

2.0.2: General Introduction

While parrots are popular pets, and there is growing interest in maintaining captive populations of parrots for research in comparative psychology labs, relatively little is known about the socio-ecology of wild parrots (Forshaw, 1989, Juniper and Parr, 2003); particularly the Neotropical species (Kroodsma and Miller, 1996). Approximately 350 parrot species are distributed throughout the world, with roughly 145 species found in tropical and sub tropical lowland forests in Neotropical regions of South America (Forshaw, 1989, Juniper and Parr, 2003). Although a number of studies provide detailed accounts of the behaviours of wild Neotropical parrots, many of these studies tend to be restricted to conspicuous species that inhabit relatively accessible locations, such as open savannah, farmlands and dry forest (Galetti and Rodrigues, 1992, Martuscelli, 1995, Waltman and Beissinger, 1992) or exposed clay-licks, where parrots regularly visit to consume soil (Burger and Gochfeld, 2003, Gilardi and Munn, 1998). In contrast to open and dry habitats, where birds can be clearly and more easily observed, lowland habitats are often characterised by closed canopies with dense vegetation, and may therefore preclude more detailed behavioural observations. Hence, many Neotropical species remain largely unstudied (Gilardi and Munn, 1998, Kroodsma and Miller, 1996). Behavioural observations of captive populations of Neotropical parrots may therefore provide valuable insights into the behaviour and ecology of these species. Species raised in the wild, however, are likely to be exposed to vastly different experiences than species raised in captivity. While such experiences may make direct comparisons between captive and wild species difficult to interpret, comparisons between different species that are raised under identical conditions in captivity may alleviate some of these concerns. It may however be possible that the direction of between-species differences also vary from captivity to the wild.

The current study aims to quantify both social and foraging behaviours of captive red-shouldered macaws (*Diopsittaca nobilis*) and black-headed caiques (*Pionites melanocephala*), as well as assess within-species

relationship dynamics. To do this, two different sampling techniques were used at two different time periods; following procedures outlined by Altman (1974) and Martin and Bateson (1996). When subjects were four months old, instantaneous scan sampling (fixed interval time point sampling) procedures were used to quantify a broad variety of conspicuous behavioural states, such as foraging, playing and preening behaviours, particularly for between-species comparisons of behaviours. When subjects were 24 months old, continuous focal sampling procedures were used to quantify particularly discrete behavioural events, such as which individuals were instigating and receiving agonistic and affiliative interactions, as well as the durations of these behaviours. These interactions were then used to determine dominance hierarchies and whether pair-bonded relationships had formed. It was unclear whether pair-bonded relationships would develop due to the sex ratio of the birds that were present in our colony (which were skewed towards males).

2.1: Instantaneous Sampling

2.1.1: Methods

Procedure

Behavioural observations were conducted in subjects' home cages from 06 October 2010 - 08 April 2011. Subjects were approximately four months old when observations began and were housed in species-specific enclosures. The behaviours of all subjects from both species were recorded during a daily one-hour focal session, between 9-11am, using instantaneous sampling methods (Altmann, 1974). Observations comprised of 66 one-hour sessions (across 66 days). During each session, the behaviours of all individuals were recorded at five-minute intervals, equating to 12 sample points for each subject per hour, totalling 792 observations per bird. For each sample point, the experimenter recorded whether individuals engaged in certain predetermined behaviours, as described in the behavioural ethogram (see

Table 2.1). Individuals that were not engaged in any of the predetermined behaviours were classed as 'other' and not further assessed. Focal observations and recordings were counterbalanced within and between species. Individuals within direct proximity of one another (i.e. within a comparable reaching distance of 30cm for both species), that were jointly engaged in the same behaviours, were also recorded for between-species comparisons of social group sizes. Individuals that were within 30cm, but were not interacting with each other, were considered to be engaged in independent behaviours. The availability of different foods and objects were held constant between species.

Statistical analysis

All statistical analyses were two-tailed and performed in SPSS (SPSS for Mac OS X, 2007) with alpha set at 0.05. Data were summed across observational periods for analysis and checked with Shapiro-Wilk and Levene's tests for assumptions of normality and homogeneity of variance for parametric analysis. When data failed to meet these assumptions, non-parametric tests were used. Independent t-tests were used to assess species differences in frequencies of social play behaviours and the manipulation of inedible objects. Repeated measures ANOVA were used to assess preening behaviours. Independent t-tests were used to compare species foraging behaviours. Independent t-tests and Mann-Whitney tests were used to assess social behaviours. Exact tests were reported for non-parametric analyses, following the procedures outlined by Mundry and Fischer (1998). Unplanned post-hoc tests were not corrected for multiple pairwise comparisons.

Table 2.2: Descriptive behavioural ethogram

Behavioural States	Description
Social play	Non-aggressive social interactions involving chasing, acrobatic swinging and wrestling
Manipulation of inedible objects	Grasping of detached objects with claws or beak, and destruction of inedible materials
Preening	Grooming of self or others (allopreening)
Drink water	Ingesting water from dispenser
Fruit and nut forage	Ingesting foraging mixture containing dried fruits and nuts. This food was contained in a separate bowl that was positioned on a feeding tray, adjacent to the soak-seed bowl at the front of the cage.
Soak-seed forage	Ingesting foraging mixture containing seeds previously softened in water by animal keepers. This food was contained in a separate bowl that was positioned on a feeding tray, adjacent to the fresh fruit bowl at the front of the cage.
Fresh fruit forage	Ingesting a variety of fresh fruits placed throughout the cage, but not on the ground
Ground	Ingesting previously discarded food items from the floor of the enclosure

2.1.2: Results

(1) **Social play:** While both species were often observed to engage in play behaviours, the type and frequency of these behaviours were remarkably different between species. Caiques participated in social play significantly more frequently than macaws (caiques mean: 252.75 ± 15.90 SEM; macaws mean: 123.00 ± 12.62 SEM); Independent t-test, $t = 6.987$, $df = 6$, $p < 0.001$ (Figure 2.1). The intensity and complexity of play behaviours, although not assessed in this study, also appeared to be more rigorous in caiques. For example, caiques would often run along the ground chasing each other, and then one bird would pounce on top of another bird; pinning it to the ground. Both birds would also wrestle on the ground by rolling over each other. Caiques would also solicit play by lying upside down on the ground. These behaviours were never observed in macaws, which instead engaged in relatively moderate play behaviours, such as grasping each other's feet while climbing up the cage wall.

(2) **Manipulation of inedible objects:** Both macaws and caiques showed similar tendencies towards manipulating inedible objects (macaws mean: 97.25 ± 6.90 SEM; caiques mean: 115.50 ± 15.79 SEM); Independent t-test, $t = 1.059$, $df = 6$, $p = 0.33$ (Figure 2.2).

(3) **Preening behaviours:** The overall frequencies and direction of preening behaviours were remarkably different between macaws and caiques. Macaws engaged in preening behaviours more frequently than caiques (macaws mean: 137.25 ± 4.99 SEM; caiques mean: 27.50 ± 3.74 SEM), revealing a significant between subjects effect of species on the frequency of preening behaviours; Repeated measures ANOVA, $F_{1,6} = 99.491$, $p < 0.001$ (Figure 2.3).

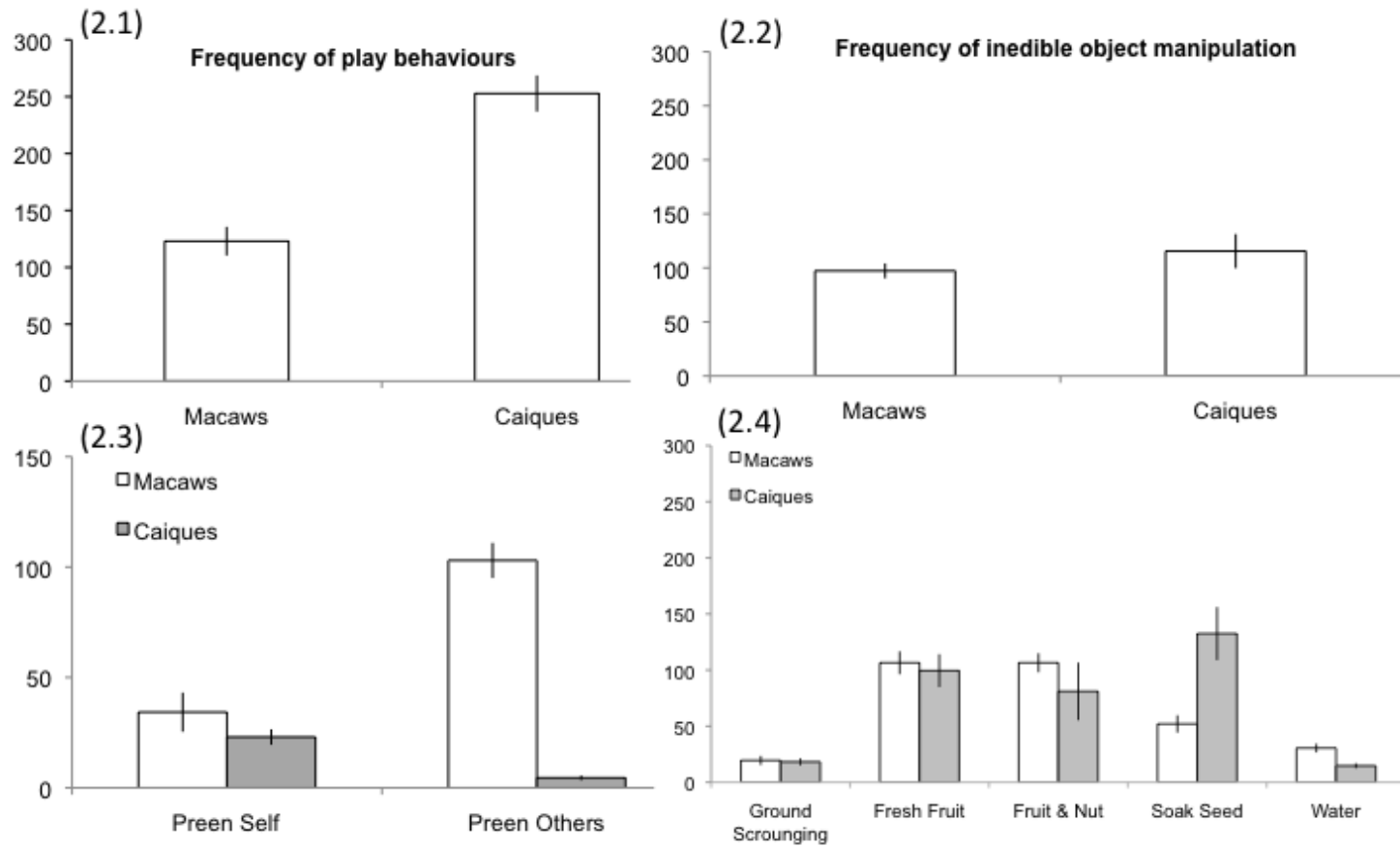
A significant within subjects effect of the type of preening behaviours; Repeated measures ANOVA, $F_{1,6} = 7.946$, $p = 0.03$, revealed that allopreening behaviours (mean = 53.75 ± 18.98 SEM) were observed more frequently than self-preening behaviours (mean = 28.63 ± 4.90 SEM).

However, a significant within subjects interaction between species and the type of preening behaviours was also observed; Repeated measures ANOVA, $F_{1,6} = 18.430$ $p = 0.005$, suggesting that frequencies of self preening and allopreening behaviours differed between species (Figure 2.3). Planned, uncorrected, post-hoc tests revealed no between-species differences in frequencies of self-preening behaviours (macaws mean = 34.25 ± 8.86 SEM; caiques mean = 23.00 ± 3.51 SEM); independent t-test, $t = 1.131$, $df = 6$, $p = 0.301$, however, macaws preened others significantly more frequently than caiques preened others (macaws mean = 103 ± 7.96 SEM; caiques mean = 4.5 ± 1.04 SEM); independent t-test, $t = 12.273$, $df = 6$, $p < 0.001$. No differences between self and allopreening behaviours were observed for caiques; paired t-test, $t = 1.329$, $df = 3$, $p = 0.276$, although, macaws preened others significantly more frequently than themselves; paired t-test, $t = 4.273$, $df = 3$, $p = 0.024$.

(4) **Foraging behaviours:** As depicted in Figure 2.4, macaws were observed at the water dispenser more frequently than caiques (macaws: mean = 30.5 ± 3.95 SEM; caiques: mean = 14.75 ± 2.21 SEM); Independent T-test, $t = 3.48$, $p = 0.013$, while caiques visited the Soak Seed feeder more frequently than macaws (macaws: mean = 52 ± 7.71 SEM; caiques: mean = 132.5 ± 23.66 SEM); Independent T-test, $t = 3.235$, $p = 0.018$. However, there were no between-species differences in frequencies of visits to the Fruit and Nut feeder (macaws: mean = 106.5 ± 8.46 SEM; caiques: mean = 81 ± 25.68 SEM); Independent T-test, $t = 0.943$, $p = 0.382$, Fresh Fruit (macaws mean = 106.5 ± 10.21 SEM; caiques mean = 99.5 ± 14.68 SEM); Independent T-test, $t = 0.392$, $p = 0.709$, or Ground foraging (macaws mean = 19.5 ± 4.03 SEM; caiques mean = 18.25 ± 3.20 SEM); Independent T-test, $t = 0.243$, $p = 0.816$.

(5) **Sociality:** As depicted in Figure 2.5, caiques engaged in solitary activities significantly more frequently than macaws (macaws mean = 348.3 ± 20.03 SEM; caiques mean = 457.25 ± 7.44 SEM); independent t-test, $t = 5.101$, $df = 6$, $p = 0.002$, whereas macaws were observed in pairs significantly more than caiques (macaws mean = 326 ± 13.34 SEM; caiques mean = 281.5 ± 3.86 SEM); Mann-Whitney Test, $U = 2.337$, $N_1 = 4$, $N_2 = 4$, $p = 0.029$.

However, no between-species differences for groups of three individuals were revealed (macaws mean = 111.75 ± 7.42 SEM; caiques mean = 95.25 ± 4.09 SEM); independent t-test, $t = 1.947$, $df = 6$, $p = 0.099$. Although, macaws were observed in groups of four more frequently than caiques (macaws = 73; caiques = 21).



Figures 2.1: Frequencies of play behaviours for macaws and caiques; **2.2:** Frequencies of inedible object manipulation for macaws and caiques; **2.3:** Frequencies of preening behaviours of macaws and caiques; **2.4:** Frequencies of foraging behaviours of macaws and caiques.

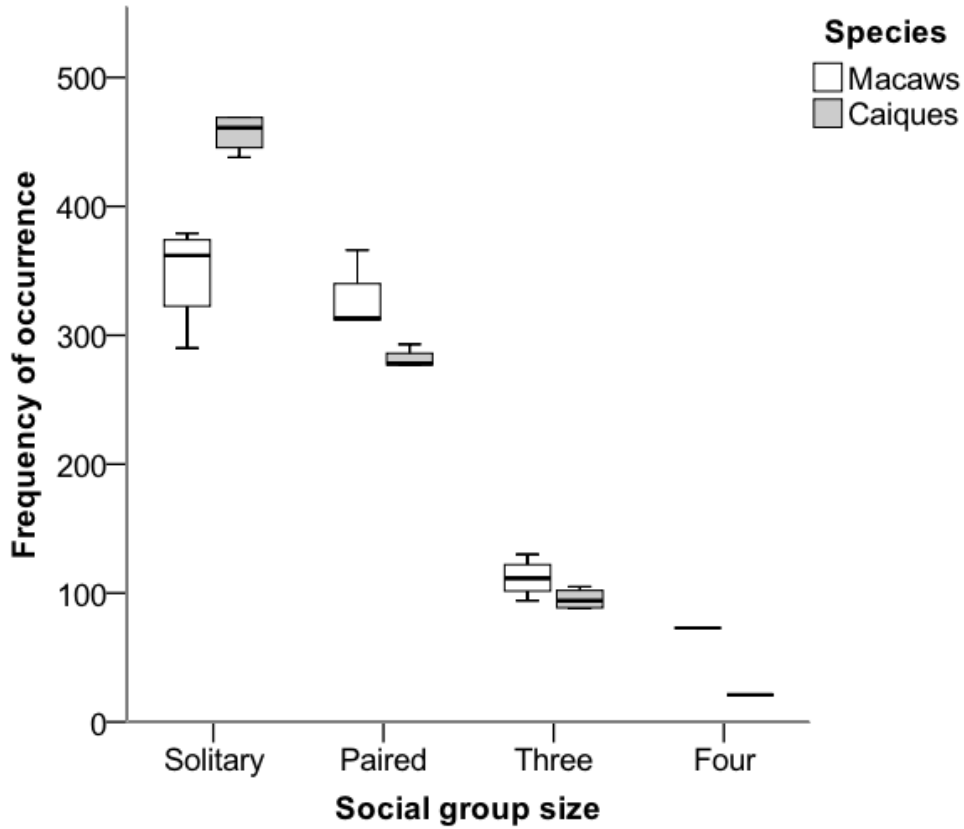


Figure 2.5: Box & whisker plot depicting median and 25-75% interquartile range of frequencies of social interactions in macaws and caiques. Frequencies of social interactions for macaws are always presented on the left hand side to those of caiques.

2.1.3: Discussion

Observations revealed general similarities in the foraging behaviours of macaws and caiques, but pronounced differences in their social behaviours. While both species showed similar propensities for inedible object manipulation, and their dietary preferences were largely equivalent, caiques consumed Soak Seed more frequently than macaws; suggesting that captive macaws and caiques may have particular dietary preferences. Macaws also visited the water dispenser more frequently than caiques. However, it is likely that caiques supplemented their water intake by consuming a relatively greater quantity of Soak Seed mixture, and hence both species may share similar requirements for water. Caiques also engaged in social play behaviours more frequently than macaws. Macaws, on the other hand, engaged in allopreening behaviours more frequently than caiques; while no between-species differences were observed in the frequencies of self-preening behaviours. Hence, macaws preened others more than they preened themselves, whereas caiques preened others as frequently as they preened themselves. Between-species differences in social group size were also observed. Caiques engaged in solitary behaviours more frequently than macaws. Macaws, in contrast, were observed in pairs more frequently than caiques. There were however no between-species differences for groups of three individuals, although it appears that macaws may also spend more time together as a group of four individuals than compared to caiques.

While macaws and caiques show few between-species differences in their dietary preferences, differences in their social behaviours appear more fundamental. Both species engage in affiliative social interactions through preening and playing behaviours. Such behaviours may help stabilise the social dynamics of a group by reinforcing social bonds between individuals, and therefore play an important role in the development and maintenance of social hierarchies (Diamond et al., 2006). However, both playing and preening behaviours are distinctly different in their expression. Play behaviour is vigorous and may be comprised of complex motor actions. As such, play behaviours may help refine coordination and dexterity and hence aid in the

manipulation of objects or extractive foraging techniques (Bekoff and Byers, 1998). However, the play behaviours observed in this study were generally socially oriented and did not frequently involve objects. Preening behaviours, by contrast, consist of gentle and delicate actions, often directed towards sensitive and vulnerable areas such as around the eyes or under the wings (personal observation). Hence preening may invoke elements of 'trust' or companionship that may not be reinforced by play behaviour. Although the greater intensity of play behaviours observed in caiques does not appear to correspond with greater propensities to manipulate inedible objects, caiques may instead use play behaviours to reinforce their social relationships; in lieu of their relatively limited allopreening behaviours. In contrast, high frequencies of allopreening and sociality suggest that macaws may form stronger social relationships than caiques. Alternatively, social development rates may also differ between these two species. As play behaviours are often characteristic of juveniles rather than adults (Bekoff and Byers, 1998), macaws may have developed their social behaviours earlier than caiques. Hence, this observational period may have missed a critical developmental period where play behaviours were more common in the behavioural repertoire of macaws. However, this explanation may be unlikely as parrots generally have prolonged developmental periods as a result of their relatively large brain size (Iwaniuk and Nelson, 2003). Moreover, parrots do not generally fledge (leave their nest), until they are at least three months of age. Hence, at four months old both species are likely to retain their juvenile characteristics.

Social play in macaws and caiques, however, appears typical of the complex range of behaviours demonstrated by other large brained species of birds. Both macaws and caiques were observed to participate in rigorous play chases and complex reciprocal object play (Diamond et al., 2006, Fagen, 1981, Ortega and Bekoff, 1987). While this study recorded the frequencies and play bouts, further investigations into the complex motor actions of typical play behaviours among parrots may reveal whether their play behaviours are comparable to other large-brained mammalian species (Iwaniuk et al., 2001). Further investigation may also reveal whether certain socio-ecological precursors, such as the need to manipulate objects to extract food, or

differences in sociality, select for particularly pronounced play behaviours (Diamond and Bond, 2003, Diamond et al., 2006). Overall, such differences in the types of affiliative interactions between macaws and caiques may reveal differences in how social relationships are established and maintained between these two species.

Instantaneous, scan sampling procedures provide an appropriate approach to measuring a variety of conspicuous behavioural states, such as feeding, playing or preening behaviours, in which subjects may undertake for extended periods of time. Hence, this approach was useful to determine broad between-species differences. However, one limitation to this approach is that such procedures may miss some of the more subtle interactions between individuals, such as the direction of instigated or received aggressive displacements, which may only last for brief durations. In the following section I use a more appropriate method for assessing particularly discrete behavioural events. Continuous focal sampling procedures were therefore used to quantify affiliative and agonistic behaviours between individuals, as well as the durations of these behaviours (Altman, 1974, Martin and Bateson, 1996). These interactions were then used to determine the dominance ranks of individuals of each species. Observations were undertaken when subjects were 24 months old in an attempt to reveal how individual relationships had stabilised over time.

2.2: Continuous Sampling

2.2.1: Methods

Procedure

Observations of macaws and caiques were conducted at regular intervals between July and September 2012. Subjects were approximately 24 months old when observations began. The behaviours of each individual for each

species were continuously recorded with a digital video camera (JVC Everio, Model No. GZ-MG645BEK, Malaysia), between 13:00-15:00 hours, for 30 five-minute sessions (150 minutes per bird). Sampling orders were randomised across sessions. Colour-coded leg bands were used to identify individuals. Prior to data collection, subjects were first habituated to the presence of the observer. To do this, 15 preliminary observational sessions were first conducted which were not included in the analysis. Hence, the data collection period only began after the birds had been exposed to the presence of an experimenter for 15 sessions. Each subsequent observational session began after a 5-minute delay period, beginning after the arrival of the observer. The aim of this procedure was to provide detailed accounts of interactions between individuals and also allow broad comparisons of subjects between four months and 24 months of age.

Social Interactions

For each observational session, interactions with the focal bird, the direction of behaviours, i.e. whether the focal bird was the initiator or recipient, and whether these interactions were of an agonistic, affiliative or neutral nature were recorded. Interactions were considered agonistic if a bird was displaced due to aggression. Agonistic behaviours included beak lunging, biting of a conspecifics feet and foot grasping of wing or tail feathers. Distress vocalisations were typically given in response to agonistic interactions. Interactions were considered affiliative when birds engaged in social activities such as allopreening and play. Affiliative interactions never invoked distress vocalisations or immediate displacement. Behaviours were coded as neutral when birds were in close proximity of one another (i.e. within 30cm), but did not interact directly, i.e. perching, self-preening or feeding. Interactions between birds were only recorded when initial behaviours from one bird elicited a response in another bird. Hence, only mutually acknowledged interactions were used in analyses (Vervaecke et al., 2000). Frequencies of agonistic interactions between each dyad were used to determine dominance hierarchies. The duration and frequencies of affiliative behaviours between

dyads were used to quantify the strength of affiliative relationships, such as pair-bonds.

Statistical analysis

Agonistic Interactions: Frequencies of agonistic interactions that resulted in displacements or submission were used to determine agonistic dominance ranks among group members. To do this, David's Scores were calculated for each individual by assessing the proportion of wins or losses among all dyadic interactions (David, 1987, Gammell et al., 2003).

More specifically, according to Gammell (2003 pp 602): David's scores are based on "the proportion of wins by individual i in his interactions with another individual j (P_{ij}) is the number of times that i defeats j (S_{ij}) divided by the total number of interactions between i and j (n_{ij}), i.e. $P_{ij} = S_{ij}/n_{ij}$. The proportion of losses by i in its interactions with j (P_{ji}) equals $1 - P_{ij}$. If $n_{ij} = 0$ then $P_{ij} = 0$ and $P_{ji} = 0$. David's scores for each member, i , of a group are then calculated with the formula: $DS = w + w_2 - l - l_2$, where w represents the sum of i 's P_{ij} values, w_2 represents the summed w values (weighted by the appropriate P_{ij} values) of those individuals with which i interacted, l represents the sum of i 's P_{ji} values and l_2 represents the summed l values (weighted by the appropriate P_{ji} values) of those individuals with which i interacted". Hence, David's scores are based on the unweighted and a weighted sum of an individual's dyadic proportions of wins, combined with an unweighted and a weighted sum of its dyadic proportions of losses (de Vries et al., 2006). de Vries and colleagues (2006) subsequently developed a correction to P_{ij} , termed D_{ij} , which was also adopted here: $D_{ij} = (S_{ij} - 0.5)/(n_{ij} + 1)$.

David's Scores were used over other dominance indices, as they are particularly robust to data where interacting pairs show reversals in the direction of dominance; as was the case with this data (Bang et al., 2010).

Affiliative Interactions: Counts and durations of affiliative interactions were checked with Shapiro-Wilk and Levene's tests and met assumptions of

normality and homogeneity of variance for parametric analysis. Independent t-tests were used to compare between-species differences in the number and total duration of instigated affiliative interactions. All statistical analyses were conducted in SPSS (SPSS for Mac OS X, 2007).

Sociograms: To compare the development of affiliative relationships and pair-bond strength, the total frequencies of affiliative interactions between dyads were quantified for each species at approximately (a) four and (b) 24 months of age. Instantaneous sampling procedures were used to quantify affiliative interactions for subjects at four months of age, totalling 792 sample points per individual across 66 one-hour sessions. Continuous sampling procedures, totalling 150 minutes of observation time for each individual, were used to quantify the affiliative interactions of subjects at 24 months of age using the sampling procedures outlined above. As different sampling techniques and sampling durations were used to quantify social relationships between these two time periods, interpretations of any comparisons should be made with caution, as the data sets are not directly equivalent. To allow for more accurate comparisons between the two observational periods, the number of interactions within each observational period were transformed into percentages, and hence relative differences may be compared. The weight of the arrows, depicting the strength of pair-bonded relationships, were calculated to reflect the proportional strength of each relationship.

2.2.2: Results

Agonistic Interactions

There were no between-species differences in the number of instigated agonistic interactions (macaws mean = 35.5 ± 11.41 SEM; caiques mean = 41.25 ± 11.21 SEM; Table 1); Independent t-test, $t = 0.359$, $df = 6$, $p = 0.732$.

David's Scores indicate a linear agonistic rank order for both species (Table 2.2): Macaws (high to low dominance); No.8>No.5>No.2>No.4, Caiques: Gold>Red>Purple>Green.

Affiliative Interactions

There were no between-species differences in the number of instigated affiliative interactions (macaws mean = 129.5 ± 18.46 SEM; caiques mean = 98.75 ± 5.9 SEM; Table 2.3); Independent t-test, $t = 1.586$, $df = 6$, $p = 0.164$. However, macaws were observed to spend a significantly greater duration (sec) instigating affiliative behaviours than caiques (macaws mean = 2530 ± 384.40 SEM; caiques mean = 1455 ± 72.24 SEM; Figure 2.6); Independent t-test, $t = 2.748$, $df = 6$, $p = 0.033$.

Sociograms

Frequencies of affiliative interactions between each potential dyad were presented as sociograms across the two time periods. No pronounced dyadic relationships were revealed for macaws at four months old (Table 2.4), although the most frequently observed affiliative behaviours were recorded between No.4 x No.8. Macaws at 24 months old (Table 2.3), however, showed more clearly defined dyadic relationships, with the most frequent accounts of affiliative behaviours shared between No.2 x No.4, and No.5 x No.8. Still, at 24 months old, these relationships were not exclusive, as there were frequent accounts of affiliative behaviours between individuals outside these pairs (Figure 2.7).

For caiques, at four months old the most frequent affiliative interactions were between Gold x Red and Green x Purple. At 24 months, affiliative interactions between Gold x Red remained strong. However, the second most frequent occurrence of affiliative behaviours were between Red x Green, followed by Green x Purple (Figure 2.7).

Table 2.2: Frequencies of agonistic behaviours resulting in displacements, observed during 30 x 5-minute sessions per individual. David's Scores (DS), indicating agonistic dominance ranks. Rank: 1 = most dominant; 4 = least dominant.

Macaws		Receiver				Total	DS	Rank
Instigator	No.2	No.4	No.5	No.8				
No.2	X	6	11	9	26	0	3	
No.4	5	X	1	2	8	-3.27	4	
No.5	8	13	X	29	50	1.59	2	
No.8	15	22	21	X	58	1.68	1	
Total	28	41	33	40	142			

Caiques		Receiver				Total	DS	Rank
Instigator	Green	Gold	Purple	Red				
Green	X	4	2	11	17	-3.07	4	
Gold	10	X	13	8	31	2.75	1	
Purple	23	3	X	22	48	-0.12	3	
Red	25	3	41	X	69	0.45	2	
Total	58	10	56	41	165			

Table 2.3: Durations (seconds) and frequency (in parentheses) of affiliative interactions. Summed across 30 x 5 minute continuous observational sessions per individual at 24 months of age.

Macaws	Receiver				
Instigator	No.2	No.4	No.5	No.8	Total
No.2	X	828 (n=39)	464 (n=24)	541 (n=39)	1833 (n=102)
No.4	1173 (n=67)	X	322 (n=15)	615 (n=34)	2110 (n=116)
No.5	736 (n=36)	428 (n=12)	X	1431 (n=68)	2595 (n=116)
No.8	1089 (n=61)	1153 (n=46)	1340 (n=77)	X	3582 (n=184)
Total	2998 (n=164)	2409 (n=97)	2126 (n=116)	2587 (n=141)	10120 (n=518)

Caiques	Receiver				
Instigator	Green	Gold	Purple	Red	Total
Green	X	332 (n=20)	296 (n=28)	638 (n=48)	1266 (n=96)
Gold	402 (n=21)	X	198 (n=18)	1002 (n=50)	1602 (n=89)
Purple	870 (n=43)	283 (n=18)	X	370 (n=33)	1523 (n=94)
Red	645 (n=48)	531 (n=45)	253 (n=23)	X	1429 (n=116)
Total	1917 (n=112)	1146 (n=83)	747 (n=69)	2010 (n=131)	5820 (n=395)

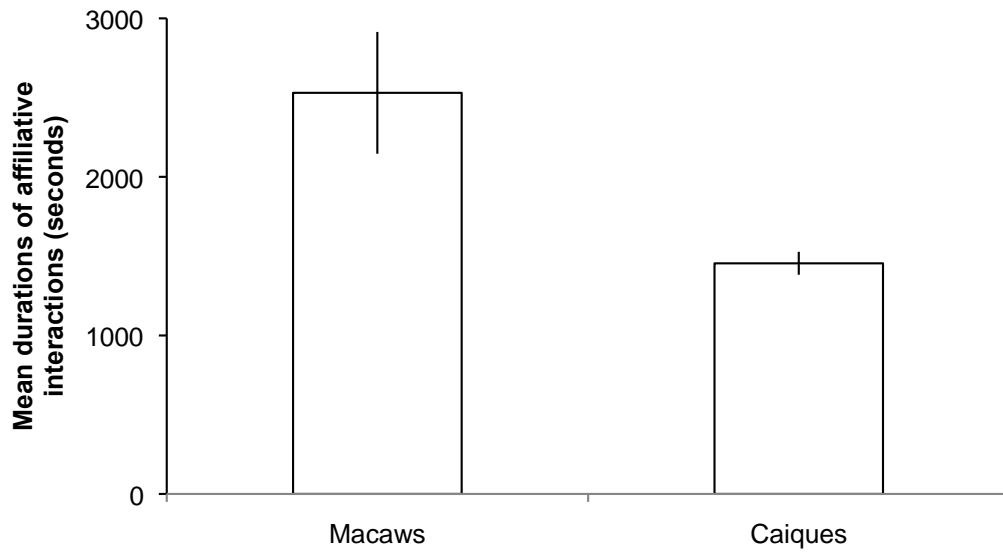


Figure 2.6: Mean duration (\pm SEM) of cumulated affiliative interactions (sec), for 30 x 5-minute observational sessions

Table 2.4: Frequencies of affiliative interactions observed at four months of age from 792 sample points per individual across 66 one-hour sessions

Macaws	No.2	No.4	No.5	No.8
No.2	X	233	267	259
No.4	-	X	192	324
No.5	-	-	X	262
No.8	-	-	-	X

Caiques	Green	Gold	Purple	Red
Green	X	154	197	167
Gold	-	X	153	231
Purple	-	-	X	168
Red	-	-	-	X

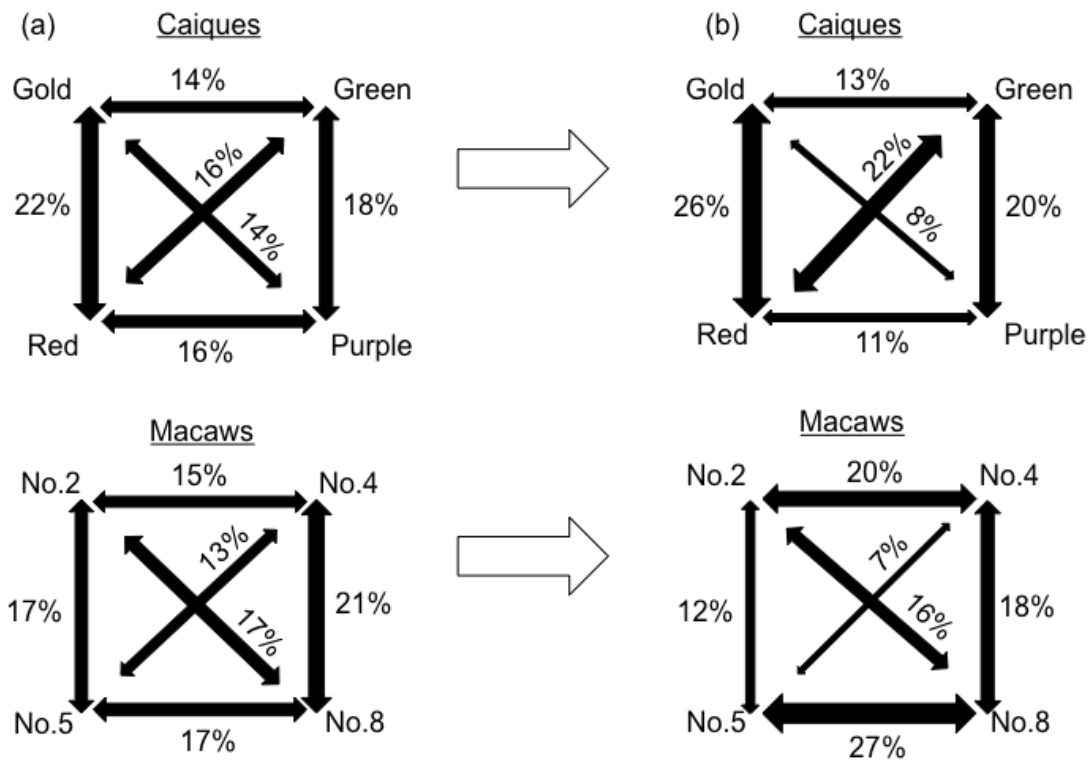


Figure 2.7: Sociograms depicting the development of affiliative relationships and pair bonds, of affiliative interactions between dyads for four macaws; No.2, No.4, No.5 and No.8 and four caiques; Green, Gold, Red and Purple at approximately (a) four months of age (instantaneous sampling procedures totaling 792 sample points for each individual) and (b) 24 months of age (continuous sampling procedures totaling 150 minutes of observations for each individual). The thickness of the arrows, and the corresponding percentage values, represent the total frequency of affiliative behaviours, and therefore pair-bond strength for each respective time period.

2.2.4: Discussion

By quantifying the affiliative and agonistic interactions of individuals for each species, broad insights into the social structure and relationship dynamics of macaws and caiques were revealed. Agonistic interactions between dyads revealed a clear linear dominance hierarchy for individuals of both species. Affiliative interactions, presented as sociograms (Figure 2.7) when subjects were four months old and again when subjects were 24 months old, show some stabilisation between early and late observational sessions, although these relationships were not exclusive. While it was not clear whether pair-bonded relationships would establish, due to the skewed sex ratio of the birds in our colony, high frequencies of affiliative interactions were generally observed between particular pairs, whereas other pairs showed lower frequencies of affiliative interactions. These relationships, however, were not necessarily exclusive, with some individuals, such as Red, showing strong affiliative relationships across multiple partners. Moreover, affiliative relationships also appear to have established irrespective of sex, as all subjects, with the exception of No.4, were male. Notably, the overall duration of affiliative interactions was greater for macaws than caiques, suggesting that macaws may be more socially attentive than caiques.

Dominance hierarchies may also correspond with the distribution of affiliative behaviours. For macaws, the most dominant individuals (No.8 & No.5) spent the most time instigating affiliative interactions, whereas the least dominant macaws (No.2 & No.4) spent the least time instigating affiliative interactions. The relationship between the durations of received affiliative interactions was however less clear. Interestingly, No.2 received the greatest amount of affiliative interactions, but spent the least amount of time instigating affiliative interactions. Caiques also shared some similarities in the structure of their affiliative interactions with macaws. Like macaws, the most dominant caique (Gold) also spent the most time instigating affiliative interactions. Moreover, the least dominant caique (Green) also spent the least time instigating affiliative interactions, but received a relatively high proportion of affiliative interactions. Interestingly, Purple spent the second longest time instigating

affiliative interactions but received a considerably lower duration of affiliative interactions than all of the other group members.

For caiques, at four months old the majority of affiliative interactions were shared between the two most dominant (Gold & Red), and the two least dominant individuals (Purple & Green). At 24 months, however, these relationships were less clear. While the majority of affiliative interactions remained stable between the two most dominant individuals, the second most dominant bird (Red) also showed a strong affiliative relationship with the least dominant bird (Green). A strong affiliative relationship, however, also remained between the two least dominant birds (Purple & Green). For macaws, at four months old the strongest affiliative relationship was between the most dominant individual (No.8) and the least dominant individual (No.4). The frequencies of affiliative interactions between all other dyads were generally similar. At 24 months however, dyadic affiliative interactions were more pronounced and predominantly occurred between the two most dominant individuals (No.8 & No.5) and the two least dominant individuals (No.2 & No.4). Such findings may however suggest that these relationships are still stabilising. Further observations taken in 6-12 months time, or more frequent sampling periods, may therefore make these relationships easier to interpret.

Overall, it appears that the most dominant macaws spent more time instigating affiliative behaviours than receiving them. Subordinate macaws, in contrast, received greater durations of affiliative interactions in proportion to the affiliative interactions that they instigated. This relationship is also observed in the most dominant (Gold) and least dominant (Green) caiques; but not for Purple, which spent a much greater proportion of its time instigating, rather than receiving, affiliative interactions, or Red, which received, rather than instigated, greater durations of affiliative interactions.

2.3: General Discussion

Observations of the study subjects were undertaken to provide a baseline of information on the social dynamics behaviours of these species. The purpose of undertaking these observations was not to present a detailed analysis of the social networks within and between these groups, but instead to provide a framework to base the following experiments. Although these observations have revealed between-species differences in particular behaviours, which may influence their propensities to interact with objects or their performances on social or physical cognitive tasks, it remains difficult to extrapolate the significance of these findings to each species' natural environment.

At four months old, individuals of each species showed no evidence of pair bonded relationships. At 24 months, however, pair-bonded relationships appeared to have stabilised, although in some individuals (Red and Green) frequent affiliative interactions were shared across multiple birds. While all caiques were male, the strength of particular homosocial relationships appeared to have developed over time. These findings suggest that, irrespective of sex, particular individuals preferred to socialise with one another, suggesting that there may have been some benefit in doing so. Homosocial relationships have been observed in captive rooks and jackdaws. Rooks that form pairs enhance their individual dominance rank compared to those that remain single (Emery et al., 2007). Bonded homosocial relationships between individuals also develop to enhance agonistic or affiliative support from a third party, as observed in some other social species of corvids (Seed et al., 2007), primates (Silk, 1999) and hyenas (Engh et al., 2005). The pair bonded relationships observed in macaws and caiques may serve similar functions. Pair bonds appeared to have developed between the two most dominant (No.8 & No.5) and the two least dominant (No.2 & No.4) macaws. Yet the relationship between dominance rank and pair bonds were inconsistent for caiques. There was, however, one female among the macaws (No.4). Although there was no evidence at 24 months that No.4 had yet reached sexual maturity, the different sex ratios between macaws and

caiques may make direct comparisons of bonded relationships social dominance ranks difficult to interpret.

The frequency of specific types of social interactions also differed between macaws and caiques. At four months, social interactions were predominantly comprised of allopreening in macaws and social play in caiques. Such findings may therefore reveal differences in how the development of social relationships establish between these species. In corvids, the unsolicited sharing of a highly valuable food form one individual to another is particularly important in the early stages of pair formation (de Kort et al., 2003, 2006). Although similar behaviours were not observed in macaws or caiques, there were infrequent occasions when two individuals engaged in mock crop feeding, a behaviour that would generally be observed between a parent and their offspring. While these behaviours were observed in macaws and caiques there was never any transfer of food between individuals. As relationships develop over time, corvids increase their allopreening behaviours, suggesting that allopreening may be used to maintain pair bonds (Emery et al., 2007). At 24 months, macaws still invested more time in affiliative behaviours than caiques. Macaws were also observed to engage in joint activities more frequently than caiques. The strength of affiliative relationships may therefore be particularly important for macaws, rather than caiques, as such relationships may serve to reduce agonistic conflicts when in a group situation, for example when foraging on a clumped distribution of resources. Such problems may however be avoided by caiques as they spend most of their time engaging in solitary behaviours. The greater strength of affiliative behaviours observed in macaws may also enhance their breeding success or defence of a nest cavity through cooperation and coordination between pairs (Emery et al., 2007). However, as little is known about the natural behaviours of these species, such speculation must be interpreted with caution.

Chapter 3: Object Interactions

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3.1: Object Neophobia

A species' natural foraging ecology may be revealed through adaptive specialisations that either promote or constrain explorative interactions with their environment. Species that inhabit environments characterised by a fluctuating supply of resources may benefit from adopting a generalised foraging repertoire. Such requirements may therefore correspond with particular behavioural traits, such as low neophobia towards objects. Conversely, high neophobia may conserve foraging specialisations, and therefore enhance foraging efficiency, in species that inhabit relatively stable environments. Intrinsic differences in object neophobia were therefore investigated in two species of parrots that possess a similar relative brain size, but naturally inhabit contrasting environments. Subjects' baseline foraging latencies, in the absence of novel objects, were compared with their latencies to retrieve food in close proximity to a series of novel objects. Subjects were tested in isolation and experienced 20 trials, each with a novel object. Foraging latencies for both species were greater in the presence of novel objects, yet red-shouldered macaws, which occur in relatively stable habitats, showed higher levels of object neophobia than black-headed caiques, which inhabit more complex environments. A wide variety of objects were used to determine whether subjects' neophobic responses could be generalised across novel objects and whether particular object characteristics influenced fear responses. While macaws became more neophobic with subsequent experience of novel objects, caiques showed some evidence for habituation to novelty, suggesting that repeated exposure to novelty during development plays an important role in how species interact with their environment. These findings suggest that the adaptive benefits of neophobia may be to conserve foraging specialisations in species that occur in habitats characterised by a predictable supply of resources.

3.1.1: Introduction

What is neophobia & how is it measured?

Neophobia is an aversion towards novel foods, objects, or places, and is generated by an uncertainty of the potential costs or benefits associated with pursuing such interactions (Greenberg, 2003). In animals, neophobia typically evokes fear responses, which may be revealed through arousal and displacement (Greenberg, 2003). The intensity of neophobia is considered to be influenced by the complexity of a stimulus, such as irregularities in shape, and its discontinuity from a familiar background (Mettke-Hofmann et al., 2006, Thorpe, 1956).

While neophobic responses towards novel places (spatial neophobia) have been assessed by comparing species' latencies to enter a novel room (Katzir, 1982, Mettke-Hofmann et al., 2009), object neophobia is generally assessed by comparing a subject's baseline retrieval latencies of a familiar food item, with retrieval latencies of the same food while in the presence of a novel object (Greenberg, 1983, 1984). These procedures can be applied across a variety of animals, both in the wild and in captivity, as well as in solitary or social settings, and may reveal consistent individual differences in neophobia. For example, mid or low ranking individuals have been found to be less neophobic than dominant individuals, which is considered a result of their relatively restricted access to resources (Katzir, 1982, 1983). Comparisons between related species that inhabit contrasting ecologies may also help broaden our understanding of the ecological mechanisms that promote adaptive differences in neophobia. As such, dietary generalists appear less neophobic than specialists, possibly because they encounter, and are required to process, a greater variety of food types while foraging (Greenberg, 1983, 1984).

While the antithesis of neophobia may be considered neophilia, an attraction towards novelty, the relationship between neophobia and neophilia remain

unclear (Greenberg, 2003). Approach and avoidance reactions may occur simultaneously, resulting in investigations that are punctuated by curiosity and fear, as observed in ravens (Heinrich, 1988) and chimpanzees (Menzel, 1963). Yet, these responses appear to vary independently from one another and hence, each response may stem from different selection pressures that may be associated with either the necessity to interact with a variety of stimuli, or a necessity to avoid potentially dangerous interactions (Greenberg and Mettke-Hofmann, 2001).

Is neophobia an ecologically adaptive trait?

Neophobia is a widespread trait, occurring across many vertebrate species, including primates, rodents, fish, reptiles and birds (Corey, 1978, Greenberg, 2003). Yet the extent of neophobia may vary considerably between closely related species with different life histories (Greenberg, 1984, 1992, Mettke-Hofmann et al., 2005, 2009, 2013), different populations of the same species (Martin and Fitzgerald, 2005), or even throughout the lifespan of individuals (Biondi et al., 2010, Heinrich, 1995b,). An individual's response to novelty may also vary according to their current social context (Coleman and Mellgren, 1994, Stöwe et al., 2006a,b), including the presence or absence of experienced (Mettke-Hofmann et al., 2006, Voelkl et al., 2006), or more dominant (Katzir, 1982, 1983, Soma and Hasegawa, 2004) individuals. Hence, social facilitation is also likely to influence neophobia. Approach and avoidance behaviours have also been found to have a heritable component, for example in great tits (Drent et al., 2003, van Oers et al., 2004), suggesting that neophobia serves a general ecological function, which may be genetically determined and subject to natural selection (Bolivar and Flaherty, 2004, Greenberg, 1992).

Two main hypotheses have been proposed to account for the selective advantages of neophobia: (1) the Neophobia Threshold Hypothesis, hereafter NTH, (Greenberg, 1990) and (2) the Dangerous Niche Hypothesis, hereafter DNH, (Barnett, 1958, Heinrich, 1988, but see Greenberg, 2003). The NTH

posits a link between neophobia and ecological plasticity. For example, species that are dietary generalists, or reside in heterogeneous environments may regularly encounter novel objects or places. Hence, the degree of their aversion towards such novelty will influence whether new resources are explored and exploited. Conversely, the DNH proposes that neophobia promotes caution when exploring novel objects, thus protecting animals from the unknown, or potential dangers of new things.

Although both hypotheses provide plausible explanations for the adaptive advantages of neophobia, there is currently greater empirical support for a relationship between neophobia and reduced behavioural flexibility, and hence the NTH (Greenberg, 2003). Mettke-Hoffman and colleagues (2002), for instance, found that parrot species, which inhabit stable, predictable habitats, were more neophobic than parrot species that inhabit more diverse and variable environments. Generalist species of warblers and sparrows also tend to be less neophobic than closely related specialists (Greenberg, 1983, 1984, 1990), and migratory garden warblers are faster, and more likely to explore novel environments than resident Sardinian warblers (Mettke-Hofmann et al., 2009). In primates, dietary generalists that rely on manipulative and explorative foraging, but which lack anatomical adaptations for such behaviours, also have relatively low levels of neophobia (Clarke and Lindburg, 1993, Day et al., 2003, Vitale et al., 1991). As such, neophobia appears to be linked to species foraging ecologies. Reliance on an ephemeral, and hence unpredictable, distribution of resources may therefore promote selection pressures that favour explorative foraging behaviours and, as a result, low neophobia. Conversely, exploration may not be necessary for survival in environments characterised by predictable or abundant resources. Hence, habitat stability may promote high levels of neophobia to conserve foraging specialisations and maintain a more efficient foraging repertoire. The extent of neophobia therefore appears to be determined by the ecological plasticity of a species (Greenberg, 2003).

Support for the NTH is however far from conclusive. In contrast to the NTH, the DNH predicts that generalist species should show high levels of neophobia as a protection mechanism to avoid the unknown dangers of new things (Greenberg, 2003). Recent studies in the wild have found that migratory New World blackbirds (Icterids) show higher object neophobia than closely related resident Icterids (Mettke-Hofmann et al., 2013). Moreover, numerous dietary generalists such as adult ravens, *Corvus corax* (Heinrich, 1988) and rats, *Rattus norvegicus* (Barnett, 1958), as well as habitat generalists such as house sparrows (*Passer domesticus*) and the shiny cowbird, *Molothrus bonariensis* (Echeverria et al., 2006), also show high levels of neophobia. However, the extent to which a species displays neophobia has also been found to vary between captive populations of resident and migratory species depending on the type of novelty experienced. While resident Sardinian warblers showed lower levels of object neophobia than migratory garden warblers (Mettke-Hofmann et al., 2005), migratory garden warblers were both faster and more likely to explore novel environments than resident Sardinian warblers (Mettke-Hofmann et al., 2009).

Neophobia also appears to be associated with developmental experience. As such, conflicting results have been reported between captive-reared and wild-reared populations of generalist (*Melospiza melodia*) and specialist (*M. georgiana*) sparrows; while wild reared specialists, tested in captivity, were more neophobic than wild reared generalists (Greenberg, 1990), captive reared specialists were less neophobic than captive reared generalists (Greenberg, 1992). Young Orange-winged Amazon parrots (*Amazona amazonica*) exposed to enriched, rather than impoverished, environments show reduced neophobia (Meehan and Mench, 2002), and the frequent rotation of objects (i.e. removal and replacement), also reduces neophobia; although, highly fearful individuals showed greater neophobic reactions when objects were more frequently rotated (Fox and Millam, 2007). The experience of novelty during the developmental period of animals in the wild may therefore play a crucial role in the extent of neophobic reactions experienced in adulthood (Biondi et al., 2010, Fox and Millam, 2004, Greenberg, 2003,

Heinrich, 1995b, Meehan and Mench, 2002). Hence, juveniles reared in simple and predictable habitats may have less to fear in their daily interactions with their environment, and therefore not develop an adaptive aversion to novelty. High neophobia may however initially protect juvenile generalists from the wide variety of potential dangers encountered during foraging, but diminish into adulthood as a result of experience (Greenberg, 1992). Conclusive support for a relationship between neophobia, ecological flexibility, and developmental experience therefore remains to be established and hence requires further investigation.

Neophobia and cognitive adaptations

The propensity to explore and flexibly adapt to novelty may also have important implications on the evolution of certain morphological and physiological traits (Mayr, 1963). Animals that avoid unfamiliar situations are unlikely to benefit from the affordances of such interactions, which may only be revealed through exploration. Such affordances may also present important selective advantages to individuals, and hence promote the evolution of certain cognitive adaptations that, for example, may enhance foraging success (Byrne, 1997). In times of food scarcity, less neophobic individuals may be more likely to incorporate novel food sources into their foraging repertoire. These individuals may, as a result, outcompete more neophobic individuals, hence promoting selection pressures that favour low neophobia. As such, neophobia has been observed to impede innovative problem-solving behaviours across a range of species, including; monkeys (Day et al., 2003), birds (Biondi et al., 2010, Bouchard et al., 2007, Seferta et al., 2001, Webster and Lefebvre, 200) and hyenas, *Crocuta crocuta* (Benson-Amram and Holekamp, 2012, 2013). However, the relationship between neophobia and innovative problem solving remains unclear. Innovative foraging behaviours correspond positively with enhanced brain size in birds and primates (Lefebvre et al., 1997, 2004, Reader and Laland, 2001, 2002). Mammals and birds with relatively larger brains are also more ecologically flexible, and demonstrate enhanced success when introduced to novel

environments (Sol et al., 2002, 2005, 2007 2008, Sol and Lefebvre, 2000). Yet there are also highly neophobic species within the corvid (Heinrich, 1988), and parrot families (Mettke-Hofmann et al., 2002) that possess particularly large brains (Iwaniuk et al., 2005), and generate innovative behaviours (Lefebvre et al., 2004, 1997). Consequently, fear may diminish substantially after animals are repeatedly exposed to stimuli that were initially novel, but become familiar through exploration, possibly because the potential for any dangerous consequences are dismissed (Heinrich et al., 1995, Menzel, 1963). Neophobia may therefore only prolong the acquisition of object interactions, and hence have no ultimate impact on the production of innovative behaviours or cognitive evolution (Greenberg, 2003).

The current study attempts to reveal behavioural adaptations that may be associated with the contrasting ecologies of red-shouldered macaws and black-headed caiques. To do this, intrinsic between-species differences in neophobia were assessed. As the rearing environment, and hence developmental experience, of both species were identical, it was possible to measure intrinsic levels of neophobia (Greenberg, 2003). Any between-species differences in neophobia may therefore suggest that such differences are genetically based, subject to natural selection and have some adaptive value (Greenberg, 1992).

Species that inhabit complex habitats may adopt more generalised foraging techniques to accommodate for the greater diversity of interactions that are required to process a variety of food types. Conversely, foraging efficiency may be enhanced in stable and predictable environments by adopting more specialised foraging techniques. Such contrasting ecologies have been found to correspond with differences in neophobia among parrots; with habitat stability resulting in higher levels of object neophobia (Mettke-Hoffman, 2002). This study, however, differs from that of Mettke-Hoffman and colleagues (2002) in a number of aspects; subjects here were raised under identical conditions, were all juveniles of a similar age group that possess a similar relative brain size, and were tested in isolation with a greater variety of novel

objects. Moreover, while Mettke-Hoffman and colleagues (2002) tested neophobia in 51 parrot species, they only assessed one red-shouldered macaw on one object, a cotton mop, and did not include black-headed caiques in their study.

Between-species differences in neophobia were assessed by comparing foraging latencies of solitary individuals in the presence and absence of novel objects (following Greenberg, 1883, 1984). Findings from this study are discussed in light of the prevailing hypotheses that attempt to explain the adaptive benefits of neophobia in birds. According to the NTH, caiques, which naturally inhabit more diverse environments than macaws, were predicted to show relatively lower levels of object neophobia. As such, caiques were expected to show shorter latencies to approach novel objects than macaws.

3.1.2: Methods

Subjects and Housing

Subjects were approximately 10 months old when tested.

Novel Objects

Subjects were individually presented with one of 20 novel objects in the following order: fluorescent box, mop-head, stone, toy mouse, cat photo, pink cup, yellow cup, roll of tape, glass jar, Ping-Pong ball, Postits (small yellow pad of paper notes), yellow pen, cable tie, green lid, white tube, black square, clear container, long container, wool, rubber band (Table 3.1, Figure 3.1).

Procedure

Subjects were tested individually between 9-11am in a visually isolated but familiar enclosure. After subjects entered the enclosure they were provided a period of five-minutes to acclimatise to the arena. A preferred piece of food of standardised size was then placed on the feeding tray inside the subject's enclosure and the subject's baseline feeding latency in the absence of novel objects was recorded (baseline control trial). If the subject did not retrieve the food within 10 min, the trial was terminated and the subject was retested the following day. Once the subject consumed the food item, the experimenter then removed any remaining food debris from the enclosure, and allowed another two-minute delay to allow the subject to settle. The experimenter then placed another preferred food item on the subject's feeding tray at 5cm to the right of a novel object (novel object trial) and recorded the subjects' latency to either retrieve the food item or interact with the novel object (following Greenberg, 1983, 1984). After 10min the novel object was removed, along with any remaining food debris. Subjects were again presented with a two-minute delay period, after which a third food item was placed on the food tray for 10 min to control for any effects of satiation from the novel object trial (second control trial). Subjects that did not retrieve the food during the novel object trial of the second control trial were allocated ceiling values of 601s. Each subject was presented with one novel object trial per day, in the above order. All trials were recorded with a digital camcorder (JVC Everio, Model No. GZ-MG645BEK, Malaysia) and subsequently scored for analysis.

Statistical Analysis

All statistical analyses were two-tailed, and performed in SPSS, with alpha set at 0.05 (SPSS for Mac OS X, 2007). Data were checked with Shapiro-Wilk and Levene's tests and log transformed prior to analysis to meet assumptions of normality and homogeneity of variance for parametric analysis. Comparisons of both between and within-species response latencies were made using Repeated measures ANOVA. To determine whether the

presence of novel objects influenced foraging latencies, control trial latencies (baseline control trials and second control trials) were compared with latencies in novel object trials, across all objects for each species. Bonferroni corrections were applied to planned post hoc tests that required multiple pairwise comparisons.

To control for any species-specific preferences for the particular food rewards, or differences in movement time (i.e. walking rather than flying), baseline control latencies were also subtracted from the novel object trial latencies where subjects retrieved food, to determine relative response latencies for between-species comparisons. To determine whether subjects habituated to novelty, comparisons between the first and last 10 objects were assessed with Repeated measures ANOVA. To do this, the relative response latencies for the first and last 10 novel object trials were averaged across subjects. The number of trials where individuals from each species retrieved the food/interacted with novel objects (classed as “Response”) were also compared with trials where there was no interaction (classed as “No Response”), using a binomial test with a probability of responding or not responding set to 0.5. To do this, individual responses were averaged across trials to avoid pseudoreplication for species comparisons.

3.1.3: Results

Latencies to retrieve a familiar food item were compared across three conditions: (1) baseline control trials, (2) novel object trials, and (3) second control trials.

Mean retrieval latencies (log transformed seconds) were greater for macaws than caiques across all conditions (Figure 3.2): baseline control trials; macaws: mean = 1.13 ± 0.15 SEM, caiques: mean = 0.68 ± 0.08 SEM; novel object trials, macaws: mean = 2.57 ± 0.09 SEM, caiques: mean = 1.50 ± 0.19

SEM; second control trials, macaws: mean = 1.98 ± 0.35 SEM, caiques: mean = 1.17 ± 0.12 SEM. These findings are confirmed by a significant main effect of species on retrieval latencies; Repeated measures ANOVA, $F_{1,6} = 12.457$, $p = 0.012$.

A significant main effect of condition (Figure 3.2); Repeated measures ANOVA, $F_{2,12} = 38.389$, $p < 0.001$, and no significant interaction between species and condition; Repeated measures ANOVA, $F_{2,12} = 2.875$, $p = 0.095$, suggests that subjects' response latencies differed depending on condition, but that each species showed similar responses to each condition. Planned comparisons revealed that subjects' response latencies were significantly greater during the novel object trials (mean = 2.04 ± 0.22 SEM) than compared to the baseline control trials (mean = 0.90 ± 0.12 SEM); Tukey test, $p < 0.001$. However latencies for novel object trials did not differ significantly from the second control trials (mean = 1.58 ± 0.23 SEM); Tukey test, $p = 0.069$. Response latencies for the second control trials were also significantly higher than baseline control latencies; Tukey test, $p = 0.007$. Subjects therefore appear to become less motivated to retrieve food over the course of the experiment. However, subjects often retrieved the food and did not appear satiated. The greater latencies in the second control trials may instead be due to a residual negative association from the previous novel object trials.

As latencies for caiques were generally shorter than those of macaws, a relative measure of neophobia was therefore required to control for any between-species differences in responses, which may be associated with food preferences or movement speed (i.e. flying as opposed to walking) rather than neophobia. To do this, subjects' baseline control trials were subtracted from their corresponding novel object trials across objects where subjects retrieved the food, and hence made a response. Relative latencies to acquire food in the presence of novel objects were greater for macaws (mean = 2.37 ± 0.13 SEM) than caiques (mean = 1.10 ± 0.19 SEM). These findings are confirmed by a significant between-species effect of relative novel object

response latencies (Figure 3.3); Repeated measures ANOVA, $F_{1,6} = 30.253$, $p = 0.002$.

However, a significant within subjects effect of novel object trial; Repeated measures ANOVA, $F_{19,114} = 7.849$, $p < 0.001$, and a significant within subjects novel object trial x species interaction; Repeated measures ANOVA, $F_{19,114} = 3.125$, $p < 0.001$, suggests that each species showed different responses to the presence of novel objects throughout the course of the experiment (Fig. 3.4). Response latencies between the first 10 and last 10 novel object trials (Fig. 3.5) increased for macaws (first 10 objects: mean = 2.24 ± 0.01 SEM; last 10 objects: mean = 2.51 ± 0.16 SEM). A planned, uncorrected comparison between the first and last 10 objects revealed a significant increase in response latencies for macaws; Paired t-test, $t = 3.773$, $df = 3$, $p = 0.033$. A decrease in response latencies between the first and last 10 objects was however observed for caiques (first 10 objects: mean = 1.45 ± 0.15 SEM; last 10 objects: mean = 0.74 ± 0.28 SEM), yet a planned, uncorrected pairwise comparison revealed no significant differences; Paired t-test, $t = 2.99$, $df = 3$, $p = 0.058$.

Overall, macaws were more likely to remain stationary (mean = 16 ± 1.15 SEM), rather than approach food (mean = 4 ± 1.15 SEM), in the presence of novel objects; Binomial test, $p = 0.012$. Caiques on the other hand were more likely to approach food (mean = 14.75 ± 1.44 SEM), rather than remain stationary (mean = 5.25 ± 1.44 SEM), in the presence of novel objects; Binomial test, $p = 0.041$ (Figure 3.6).

Table 3.1: Description of novel objects

OBJECTS	DESCRIPTION	DIMENSIONS (mm)
(1) Fluorescent box	Bright orange with a regular pattern of black numbers on the top surface.	100 x 100
(2) Mop-head	White and blue	250 x 80
(3) Stone	Grey	170 x 90
(4) Toy mouse	White	80 x 30
(5) Cat photo	Black and white	160 x 110
(6) Pink cup	Pink	Ø 50 x 80
(7) Yellow cup	Yellow	Ø 50 x 80
(8) Roll of tape	White	Ø 100 x 20
(9) Glass jar	Clear	Ø 80 mm x 70
(10) Ping-Pong ball	White	Ø 35
(11) Postits	Yellow paper notes	75 x 75
(12) Yellow pen	Yellow	130 x 10
(13) Cable tie	Black	200
(14) Green lid	Green and white	Ø 90 x 10
(15) White tube	White	Ø 25 x 70
(16) Black square	Black	20 x 20
(17) Clear container	Clear with opaque lid	Ø 20 x 60
(18) Long container	Clear with white side	100
(19) Wool	White	150
(20) Rubber band	Brown	130 x 10



Figure 3.1: Twenty novel objects that were individually presented to subjects.

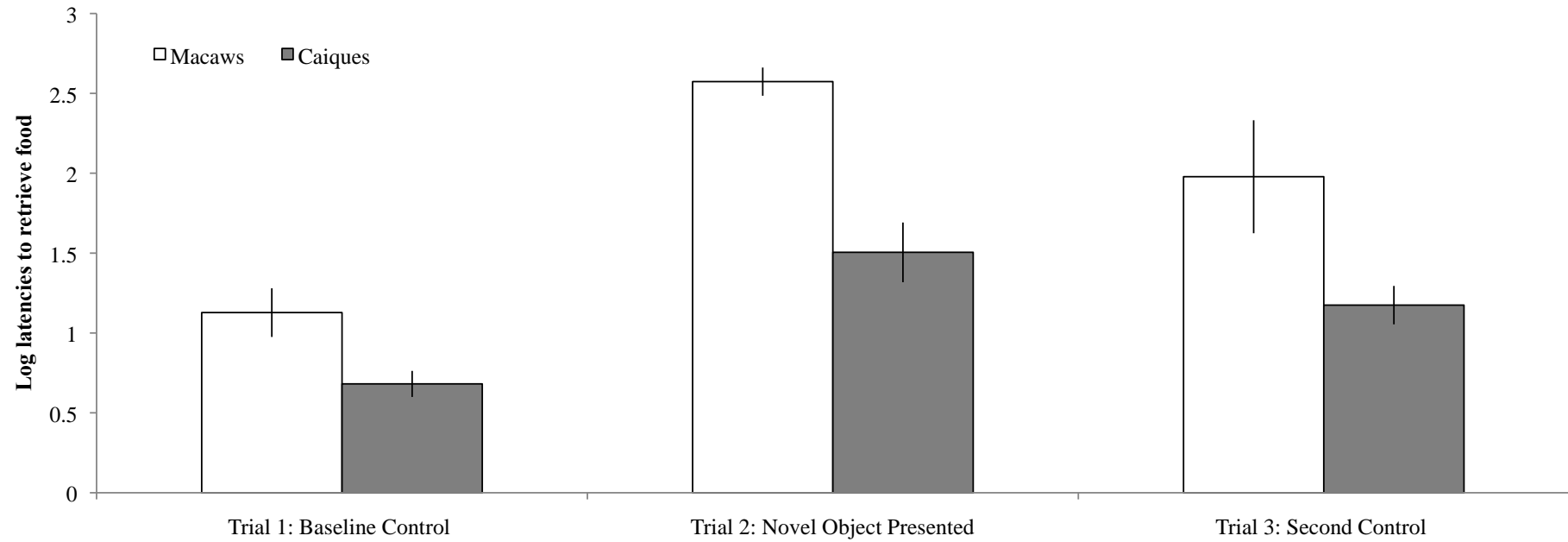


Figure 3.2: Mean log transformed latencies (\pm SEM) to retrieve food across 20 trials.

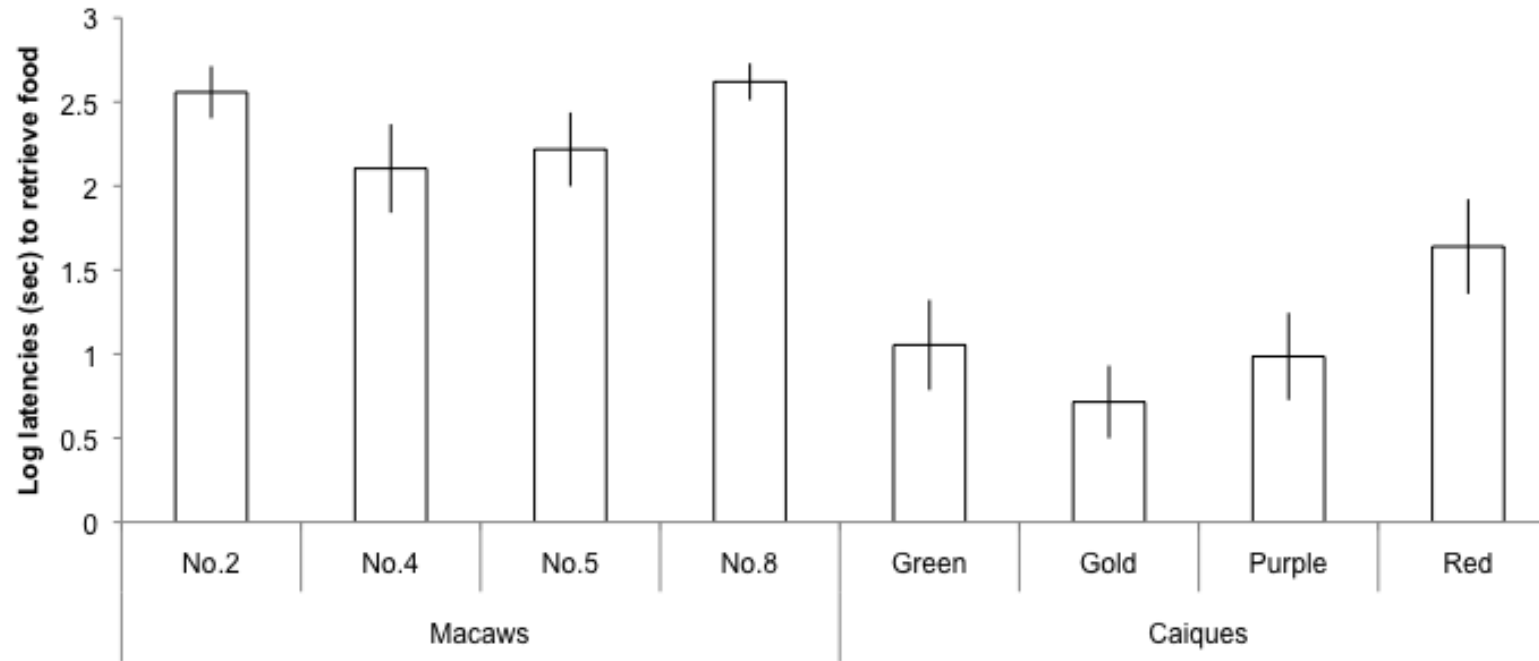


Figure 3.3: Mean log transformed relative feeding latencies (\pm SEM) of individuals in the presence of 20 novel objects.

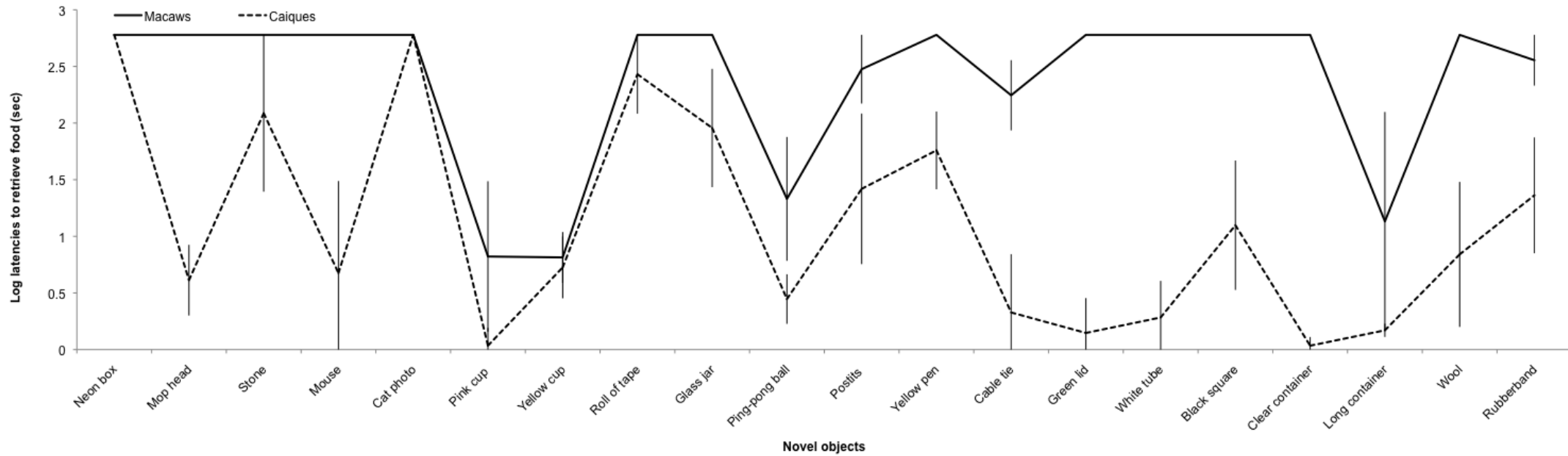


Figure 3.4: Mean log transformed latencies (\pm SEM) to retrieve a familiar food item in the presence of 20 novel objects. Baseline control latencies were subtracted from novel object trials in which subjects retrieved the food. A value of 2.78 is a result of subjects showing no response i.e., not retrieving the food during a novel object trial.

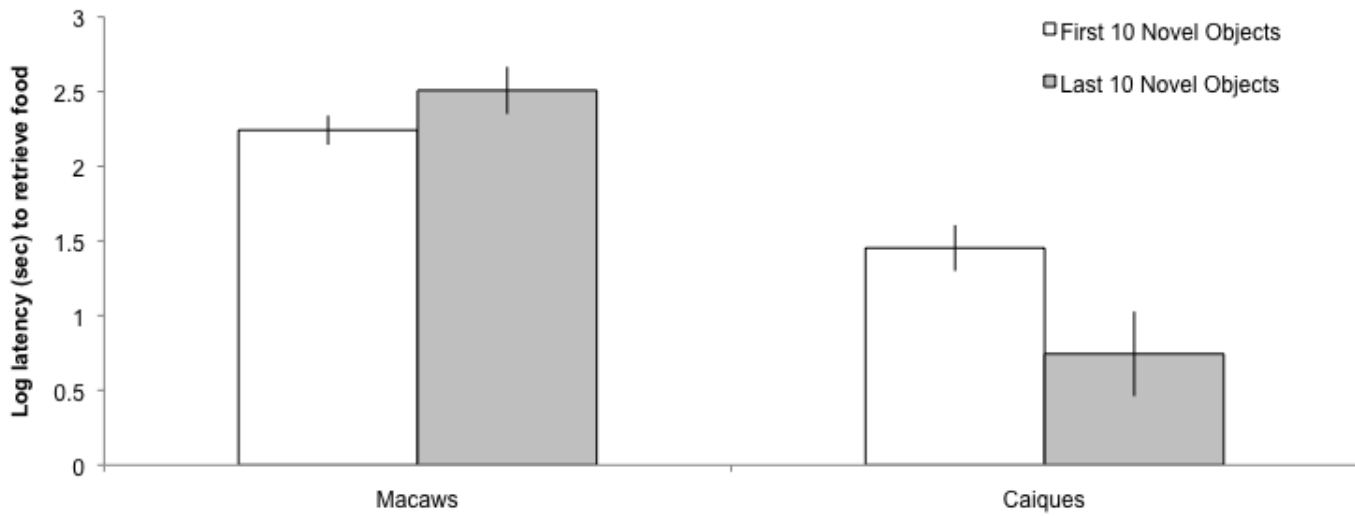


Figure 3.5: Mean log transformed relative feeding latencies (\pm SEM) for the first and last 10 novel objects.

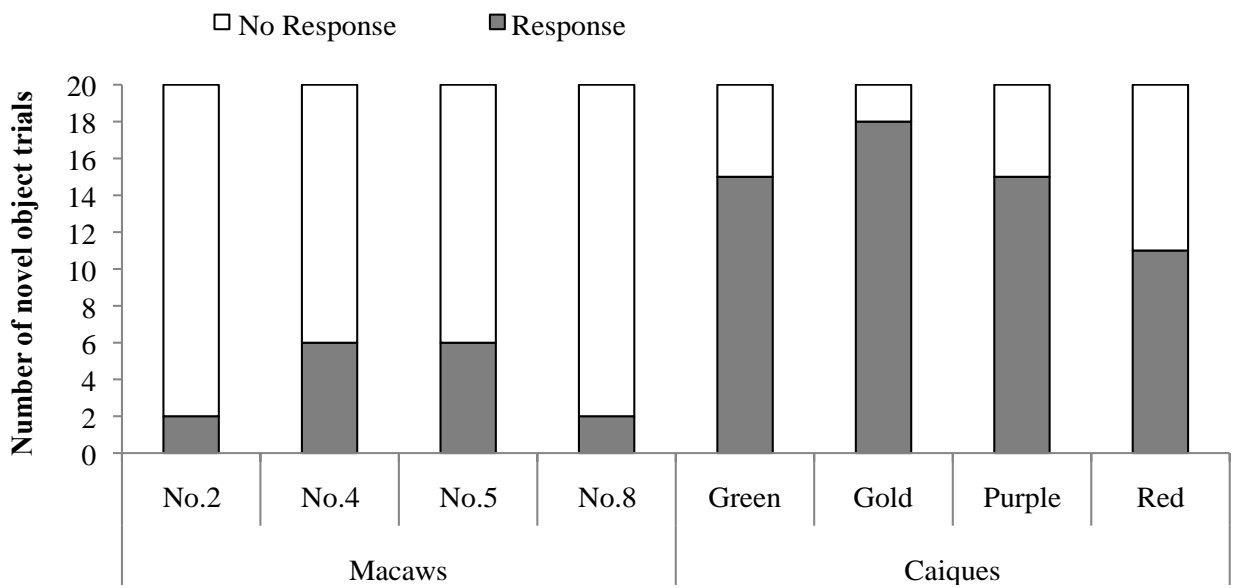


Figure 3.6: Proportion of responses to 20 novel objects.

3.1.4: Discussion

Results revealed that latencies to retrieve a familiar food item were greater for both species when food items were presented alongside novel objects, than compared to baseline foraging rates without novel objects. Moreover, between-species differences in object neophobia were also revealed. When raised under identical conditions, red-shouldered macaws, showed relatively high levels of object neophobia compared to black-headed caiques. These results may support previous findings, where species' neophobic responses coincide with adaptive response to their natural foraging behaviours, such as the need to actively search for food, or avoid dangerous encounters (Glickman and Sroges, 1966, Mettke-Hofmann et al., 2002).

Findings from the current study may therefore provide further support for the Neophobia Threshold Hypothesis (NTH), suggesting that the adaptive function of object neophobia is associated with the ecological plasticity of a species. Macaws, which inhabit environments characterised by a stable distribution of resources show higher levels of neophobia than caiques, which inhabit more variable environments. The ultimate function of neophobia may therefore be to conserve foraging specialisations, and hence maintain efficient foraging mechanisms, in species that inhabit stable environments. Species that inhabit environments characterised by greater complexity, on the other hand, may benefit from relatively low levels of neophobia, as they are required to use more generalised and flexible foraging techniques to accommodate for a greater variety and fluctuating availability of resources.

Greenberg (1992) however, revealed contrasting differences in neophobia between captive and wild reared sparrows. When raised in the wild, species that inhabit more specialised environments, such as marshes, showed higher neophobia than related species that inhabit more diverse environments. Surprisingly however, when raised in captivity, the generalist species showed higher levels of neophobia than the more specialised species. Consequently, Greenberg (1992) suggests that differences in neophobia may be due to

complex interactions with the environment, with post-fledging experience playing an important role in reducing neophobia in more diverse environments. For example, juvenile ravens (*Corvus corax*) have been observed to be more curious and neophilic than their adult counterparts (Heinrich, 1995b). While Greenberg's (1992) subjects were tested when they were approximately two months old, subjects in this study were tested at 10 months of age. However, in the current study, macaws and caiques were both reared under identical conditions in captivity, yet macaws, in comparison to caiques, showed relatively high levels of neophobia. Post-fledging experience may have reduced neophobia in caiques, whereas such experiences do not appear to have had the same influence on macaws. Evidence to support these claims may be revealed by comparing how each species' response latencies changed after successive exposure to novel objects. While habituation to novelty is generally restricted to the repeated presentation of the same object in the same location (Heinrich, 1995, Menzel, 1963), the neophobic responses of caiques appeared to decrease, albeit not significantly, as they were subsequently exposed to a greater variety of novel objects, suggesting some evidence of habituation, irrespective of object familiarity. Macaws, on the other hand, became more neophobic after experiencing an increasing variety of novel objects.

Although subjects did not experience any adverse effects associated with approaching novel objects, macaws did not learn, even after repeated experience, that novel objects were benign. Caiques on the other hand may have learned, after exploring a variety of novel objects, that novelty was not associated with adverse risk. Caiques also appear to have a greater intrinsic motivation to explore and manipulate objects than macaws (see chapter 3.2), which may contribute to lowering their levels of neophobia at 10 months of age. Hence, repeated exposure to novelty may reduce neophobia in some species, but not others. These findings provide further support for Greenberg's (1992) studies on captive-reared sparrows, as well as wild-reared warblers (Greenberg, 1983,1984) and sparrows (Greenberg, 1990), and numerous species of parrots (Fox and Millam, 2007, Meehan and Mench,

2002, Mettke-Hofmann et al., 2002), suggesting that neophobia may diminish as animals experience a variety of novel interactions in their environment, which in turn may contribute to the low levels of neophobia found in more generalist species.

While the intensity of subjects' neophobic responses appeared to be influenced by particular novel objects, only two objects were clearly avoided by both species; the neon box and the cat photo. Although the square shape of the neon box was regular and hence may not be considered complex (Mettke-Hofmann et al., 2006), it is likely that its fluorescent orange colour and pattern of numbers stood out from the background and was hence viewed as particularly novel (Thorpe, 1956). Similar findings have been revealed in warblers, which avoid brightly coloured objects in comparison to dull coloured objects (Greenberg, 1983). Moreover, the neon box was relatively large in comparison to other objects, and may therefore be approached more hesitantly than smaller objects due to its potential to conceal dangerous information; as observed in ravens (Heinrich et al., 1995), and warblers (Greenberg, 1983, Mettke-Hofmann et al., 2006). Macaws and caiques also avoided a black and white photo of a cat's face, with prominent eyes, even though they had not encountered such an animal before. These responses suggest that macaws and caiques may possess innate adaptations to help avoid dangerous encounters in their natural environment. Although some birds, such as ravens, approach fuzzy objects more cautiously than smooth objects (Heinrich et al., 1995), caiques showed little fear of objects that shared other mammalian features, such as the fake mouse, mop-head or wool. Moreover, caiques also avoided inanimate objects that had no resemblance to a mammalian predator, such as a smooth stone or roll of tape. Further investigation into which components of the cat image are particularly fear inducing, such as the presence or absence of large eyes, may be useful to confirm such interpretations. Like ravens (Heinrich et al., 1995), macaws appeared to be less fearful of small, round objects, such as the pink and yellow cups and Ping-Pong ball, in contrast to brightly coloured or fuzzy objects. However, this study revealed no obvious object relationships

as particularly fear inducing or attractive, with the exception of the fluorescent box and cat photo.

As both subjects were raised under identical conditions, such differences in neophobic reactions between macaws and caiques may therefore be considered innate, and possibly the result of contrasting selection pressures that each species face in their particular natural habitats. Such findings may also have important implications for the behavioural flexibility of these species. As brain size correlates positively with certain types of flexible behaviours, such as innovative foraging (Lefebvre et al., 2004, 1997), and neophobia has been observed to impair innovative foraging behaviours (Biondi et al., 2010, Bouchard et al., 2007, Day et al., 2003, Webster and Lefebvre, 2001), investigations that assess behavioural flexibility in macaws and caiques, which possess a similar relative brain size but show marked differences in object neophobia, may yield further support for the NTH.

The overall findings from this study reveal that red-shouldered macaws and black-headed caiques show pronounced intrinsic differences in their reactions towards novel objects. Such findings correspond with the complexity of each species' natural habitat, suggesting that the adaptive benefits of neophobia may be to maintain foraging specialisations, and hence foraging efficiency, in habitats that are characterised by an abundant and predictable supply of resources.

3.2: Familiar Object Exploration

Object exploration was investigated to determine whether any between-species differences in behaviours reveal particular adaptive specialisations that may be associated with the contrasting ecologies of each species. Forty-eight wooden objects of different sizes, shapes and colours were repeatedly presented to each species in their home cages. Solitary object exploration was then quantified for each individual. Social aspects of object interactions were also recorded, including the order of within-group first-touch object interactions, as well as affiliative and aggressive object interactions. Caiques required fewer sessions than macaws to first interact with the objects, suggesting reduced neophobia in caiques compared to macaws. Overall, caiques also interacted with a greater number and diversity of objects than macaws, possibly revealing that caiques are more neophilic than macaws. Both species showed preferences for certain colours, shapes and sizes, of objects. While there were no individual differences in frequencies of first-touch object interactions among macaws, individual differences were more pronounced among caiques. That is, for caiques, but not macaws, certain individuals were more frequently observed to initiate object exploration. The majority of object interactions for both species were of an affiliative, rather than aggressive, nature, revealing that parrots engaged in joint object exploration more frequently than they usurped objects from one another. Differences in the extent of object exploration between macaws and caiques may suggest that each species has evolved particular adaptive responses to accommodate for ecological challenges that are associated with their natural habitats.

3.2.1: Introduction

Animals that inhabit environments characterised by a fluctuating supply of resources may benefit from a diet that consists of a wide variety of food types. Conversely, in environments that are characterised by a stable and abundant distribution of resources, animals may enhance their foraging efficiency by specialising on a restricted variety of food types that can be easily located and processed (Cockburn, 1991). Hence, different foraging ecologies may require animals to seek out different information about their environment, which may in turn correspond with certain behavioural or cognitive adaptations (Glickman and Sroges, 1966, Platt et al., 1996). As a result, the necessity to process numerous types of food may promote enhanced exploratory behaviours in species that are dietary generalists, rather than specialists (Day et al., 2003, Tebbich et al., 2009, Webster and Lefebvre, 2000), or species that inhabit relatively complex, rather than predictable, habitats (Mettke-Hofmann et al., 2002)

A species' foraging ecology may therefore result in particular cognitive adaptations that have evolved to enhance their foraging efficiency. Species that depend on spatially demanding foraging behaviours, such as those in the food-caching family Corvidae for example may enhance their foraging success by accurately remembering the location of particular food items, across both time and space (Clayton and Dickinson, 1998). The adaptive value of these specialisations in spatio-temporal memory may then be revealed experimentally. For example, specialised food-storing corvids show more accurate performances on spatial memory tasks than less specialised food-storing corvids (Balda and Kamil, 1989). Cognitive specialisations may also allow species to respond flexibly to environmental changes, such as a variable climate and hence ephemeral food supply. As such, food storing mountain chickadees (*Poecile gambeli*) that inhabit regions with relatively demanding foraging conditions are more accurate at retrieving their caches than those individuals that inhabit more stable environments (Pravosudov and Clayton, 2001). Moreover, neuroanatomical adaptations for enhanced spatial

memory, such as an enlarged hippocampus in food-storing passerines in contrast to non-food-storing species, may also support such findings (Krebs et al., 1989).

Exploratory behaviours have been found to be consistent among individuals (Cole et al., 2011, Dingemanse et al., 2002, Morand-Ferron et al., 2011a, Verbeek et al., 1994), and heritable (Dingemanse et al., 2002, Drent et al., 2003) in species such as great tits (*Parus major*), suggesting a selective advantage to individuals under certain ecological conditions (see also Pravosudov and Clayton, 2001). Exploratory behaviours may help animals locate ephemerally distributed or concealed familiar foods, or provide useful information about changes in the abundance of essential resources, such as nesting materials. Exploration may also be used to gather information about novel resources, which may be particularly beneficial in times of resource scarcity. However, the affordances of novelty may only be revealed after approaching and possibly engaging in a potentially dangerous interaction. While exploratory behaviours may be driven by a necessity to discover new resources, new locations of familiar resources, or even new methods for obtaining familiar resources, these behaviours appear to be regulated by an interaction between certain psychological mechanisms, such as an attraction to, or fear of novelty; neophilia and neophobia respectively (Greenberg, 2003). Hence, neophobia may be associated with the costs of exploration, e.g. risk of predation or ingesting toxic foods, whereas neophilia may be driven by the adaptive benefits of exploration (Greenberg and Mettke-Hofmann, 2001). While object neophobia is generally assessed by comparing an animal's latency to retrieve a familiar food item in the presence and absence of a novel object (Greenberg, 1983, 1984), neophilia, on the other hand, is assessed by measuring the extent of object exploration independent of the presence of food (Glickman and Sroges, 1966, Heinrich, 1995b, Mettke-Hofmann et al., 2002, Tebbich et al., 2009).

Comparisons of object exploration may therefore be systematically quantified across a variety of species with contrasting ecologies to reveal whether

exploration has developed under adaptive selection pressures in response to particular environmental challenges. Consequently, foraging behaviours that require extensive manipulation of the environment appear to favour the development of sustained investigatory activities, whereas readily available foods, requiring minimal effort for acquisition do not (Day et al., 2003, Glickman and Sroges, 1966, Mettke-Hofmann et al., 2002, Tebbich et al., 2009).

In the current study, propensities for object exploration are compared between two species of Neotropical parrots, which naturally inhabit environments of contrasting complexity. As such, environmental complexity is considered a measure of the diversity of habitats used by each species, which may also include a wider variety, and fluctuating availability, of food types (Godfrey-Smith, 2002). However, little is known about the foraging ecologies of these species. Red-shouldered macaws (hereafter macaws) occur in stable, open wooded habitats and savannahs, whereas black-headed caiques (hereafter caiques) prefer more complex, heterogeneous habitats comprised of closed canopy and forest edges (Juniper and Parr, 2003); see Chapter 1.4 for a more detailed description of each species known natural history.

Species that inhabit complex habitats may therefore adopt more generalised foraging techniques to accommodate for variation in the availability of resources, therefore showing relatively high levels of object exploration and hence neophilia. Conversely, foraging efficiency may be enhanced in stable and predictable environments by adopting more specialised foraging techniques. Such species may therefore show low levels of object exploration and hence low neophilia and high neophobia. The contrasting ecologies of macaws and caiques therefore predict that caiques will be more explorative, and hence interact with a greater abundance and diversity of objects than macaws, as they may be required to adopt such strategies to accommodate a greater diversity of challenges in their natural foraging environment. Conversely, macaws may be less explorative than caiques as their natural

habitats appear more predictable and stable, and therefore may require relatively fewer exploratory behaviours.

3.2.2: Methods

Experimental Procedure

Subjects were tested in social groups in their home cages, and presented with objects every 2-3 days to maintain high levels of motivation. Sessions began with the presentation of 48 objects (Figure 3.7), comprised of yellow, blue and red wooden balls (4 sizes), rings (3 sizes), sticks (5 sizes) and cubes (3 sizes). Objects were randomly assorted and presented on the cage floor.

I recorded the characteristics of each object that the subjects explored, as well as the frequency of all object interactions. For both species, the: (1) number, (2) diversity, (3) colour, (4) shape and (5) size of objects that each subject interacted with were recorded. Social aspects of object exploration, such as the: (6) ranked order of objects first touched, and (7) type of social object interactions, such as the number of times an object was stolen from another bird (negative) and the number of times subjects participated in shared object manipulations (positive) were also recorded for each individual. To ensure a more intrinsic measure of individual object exploration, only solitary object interactions were analysed, rather than social object manipulations. That is (with the exception of 7 above), if one bird began interacting with an object, and then another bird joined in, only the first bird's interaction was recorded.

In an attempt to control for between-species differences in object neophobia, trials commenced for each species after a respective individual first interacted with any of the objects. Each species was then presented with 15 x 30minute

sessions. Sessions were video recorded (JVC Everio, Model No. GZ-MG645BEK, Malaysia). Recordings were taken from outside the subjects' cage and were supplemented by verbal annotations of behaviours by the observer. Recordings were subsequently coded for analysis.

Statistical Analysis

All statistical analyses were two tailed and conducted using SPSS (SPSS for Mac OS X, 2007). Data were checked with Shapiro-Wilk and Levene's tests prior to analysis for assumptions of normality and homogeneity of variance for parametric analysis. Data that failed to meet these assumptions were analysed with non-parametric tests. Repeated measures ANOVA were used to assess between-species differences in frequencies of object interactions, the diversity of objects manipulated and social object interactions, i.e. shared (positive) and stolen (negative) object interactions. Within-species object interactions were compared using non-parametric Friedman Tests. Post-hoc tests were made using paired t-tests and Wilcoxon Signed Ranks Tests. Subjects' interactions with different colours, shapes and sizes, as well as social object-interactions, were averaged across the 15 sessions prior to analysis. Ranked orders of individuals' first touch object interactions for each session were not included in statistical analyses, but interpretations of descriptive statistics are discussed. Between-species comparisons of the number of sessions where subjects showed no response to the objects were made with independent t-tests. Exact tests are reported for all non-parametric analyses, following the procedures of Mundry and Fischer (1998).

3.2.3: Results

Caiques first began interacting with objects during their second 30-minute presentation. Purple and then Red were the first individuals to interact with objects. Gold and Green first interacted with objects on the third and fourth presentations respectively. All of the macaws began interacting with the objects on their ninth 30-minute presentation in the following order: No.4, No.2, No.5, No.8. To simplify the information presented in this section selected means and SEM are only reported with their associated figures and not the text.

(1) **Frequency of object interactions (Figure 3.8a,b):** Caiques interacted with a greater number of objects per session than macaws (caiques: mean = 17.08 ± 3.62 SEM; macaws: mean = 2.42 ± 0.26 SEM), revealing a significant between subjects effect of species; Repeated measures ANOVA, $F_{1,6} = 16.299$, $p = 0.007$. A significant within subjects effect of session; Repeated measures ANOVA, $F_{14,84} = 1.928$, $p = 0.034$, and a significant within subjects interaction between session x species; Repeated measures ANOVA, $F_{14,84} = 1.99$, $p = 0.028$, suggests that a greater number of objects were explored during later rather than earlier sessions and that frequencies of object exploration in later sessions varied according to species (Figure 3.8a). A planned post-hoc test however revealed no significant differences in frequencies of object interactions between early (sessions 1-5 averaged, mean = 9.80 ± 6.96 SEM) and late sessions (sessions 10-15 averaged, mean = 22.5 ± 1.60 SEM) for caiques; paired t-test, $t = 2.299$, $df = 3$, $p = 0.105$. However, as the variation across subjects was quite high, these findings suffer from low power (Observed Power = 0.36). A significant effect may therefore be revealed with a larger sample size. Post-hoc tests on the frequency of object interactions for macaws were not conducted, as subjects' interactions appeared to remain consistently low across sessions (Figure 3.8a).

(2) **Diversity of object interactions (Figures 3.9ab):** A significant between subjects effect of species on the diversity of object interactions; Repeated measures ANOVA, $F_{1,6} = 12.042$, $p = 0.013$, reveals that caiques interacted with a greater diversity of objects per session than macaws (caiques: mean = 8.35 ± 1.95 SEM; macaws: mean = 1.53 ± 0.19 SEM; Figure 3.9a). A significant within subjects effect of session; Repeated measures ANOVA, $F_{14,84} = 3.025$, $p = 0.001$, and a significant within subjects session x species interaction; Repeated measures ANOVA, $F_{14,84} = 2.63$, $p = 0.003$, suggests that a greater diversity of objects were explored during later rather than earlier sessions, and that frequencies of object exploration in latter sessions varied according to species. A planned post-hoc test supports these interpretations, revealing that caiques explored a greater diversity of objects in latter sessions (sessions 11-15 averaged, mean = 11.90 ± 1.09 SEM) than compared to earlier sessions (sessions 1-5 averaged, mean = 4.30 ± 3.12 SEM); paired t-test, $t = 3.241$, $df = 3$, $p = 0.048$. Post-hoc tests on the diversity of object interactions for macaws were not conducted, as subjects' interactions appeared to remain consistently low across sessions (Figure 3.9b).

(3) **Colour (Figure 3.10):** Macaws showed no significant preferences for certain colours of objects; Friedman Test; $\chi^2 (2, N = 4) = 6.00$, $p = 0.69$. Caiques also showed no significant preferences for particular colours of objects; Friedman Test; $\chi^2 (2, N = 4) = 1.714$, $p = 0.519$.

(4) **Shape (Figure 3.11):** Macaws showed no significant preferences for certain shapes of objects; Friedman Test; $\chi^2 (3, N = 4) = 5.40$, $p = 0.158$.

Caiques however, showed a significant preference for particular shapes of objects; Friedman Test; $\chi^2 (3, N = 4) = 11.100$, $p = 0.001$. However, an unplanned, uncorrected post-hoc test, based on descriptive statistics, revealed no significant differences in frequencies to interact with Rings and Cubes; Wilcoxon Signed Ranks Test, $z = 1.826$, $N - \text{Ties} = 4$, $p = 0.125$,

suggesting that any further comparisons would also yield non-significant results.

(5) Size (Figure 3.12): Macaws showed significant within subjects' preferences for Rings; Friedman Test; $\chi^2 (2, N = 4) = 6.50, p = 0.04$; Sticks; Friedman Test; $\chi^2 (4, N = 4) = 14.60, p < 0.001$; and Balls; Friedman Test; $\chi^2 (3, N = 4) = 10.543, p = 0.002$. Unplanned, uncorrected Wilcoxon Signed Ranks post-hoc tests, however, revealed no significant size preferences for any of the above objects. No significant within subjects size preferences were observed for Cubes; Friedman Test; $\chi^2 (2, N = 4) = 1.714, p = 0.519$.

Caiques showed significant within subjects' preferences for the size of: Sticks; Friedman Test; $\chi^2 (4, N = 4) = 11.494, p = 0.006$; and Balls; Friedman Test; $\chi^2 (3, N = 4) = 8.289, p = 0.021$. Unplanned, uncorrected Wilcoxon Signed Ranks post-hoc tests, however, revealed no significant size preferences any of the above objects. No significant within subjects' size preferences were observed for Rings; Friedman Test; $\chi^2 (2, N = 4) = 2.00, p = 0.431$; or Cubes; Friedman Test; $\chi^2 (2, N = 4) = 4.933, p = 0.102$.

(6) First touch interactions (Figure 3.13): The ranked order of first touch object-interactions among macaws appears to be more evenly distributed across individuals than compared to caiques. That is, for macaws, all individuals showed similar tendencies for first touch object interactions. Caiques, on the other hand, showed more consistent individual differences in the ranked order of their first touch interactions with the same individual tending to interact first with any given object. Across the 15 sessions, Purple and then Green were frequently the first individuals to interact with objects (Purple on 7 occasions; Green on 6 occasions). Gold initiated object interactions on two occasions, whereas Red was never the first bird interact with objects. Instead, Red was more often ranked as the second (4 occasions) or third (7 occasions) bird to interact with objects. The number of sessions where subjects showed no response to any of the objects was

significantly higher for macaws (mean = 5.75 ± 0.63 SEM) than caiques (mean = 2.25 ± 0.85 SEM); Paired t-test, $t = 3.30$, $df = 6$, $p = 0.016$.

(7) **Social Object Interactions (Figure 3.14a,b,c)**: No significant between subjects effect of species on social object interactions (shared versus stolen interactions) was observed; Repeated measures ANOVA, $F_{1,6} = 0.482$, $p = 0.513$.

The majority of social interactions, for both species, were shared, rather than stolen, revealing an overall within subjects effect of social object interactions; Repeated measures ANOVA, $F_{1,6} = 69.506$, $p < 0.001$. No within subjects interaction of social object interactions x species; Repeated measures ANOVA, $F_{1,6} = 0.185$, $p = 0.882$, however, suggests that macaws and caiques showed similar social behaviours, as revealed from the descriptive statistics.

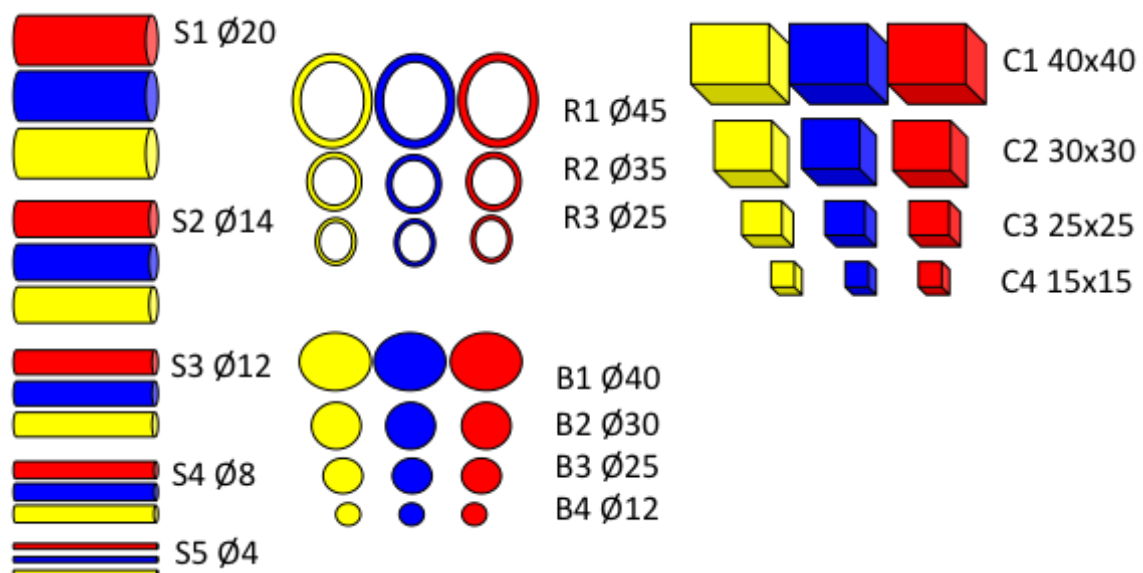


Figure 3.7: Schematic of wooden objects presented for exploration (dimensions in mm); Sticks: S1-S5; Cubes: C1-C4; Balls: B1-B4; Rings: R1-R3. Sticks were 80mm long.

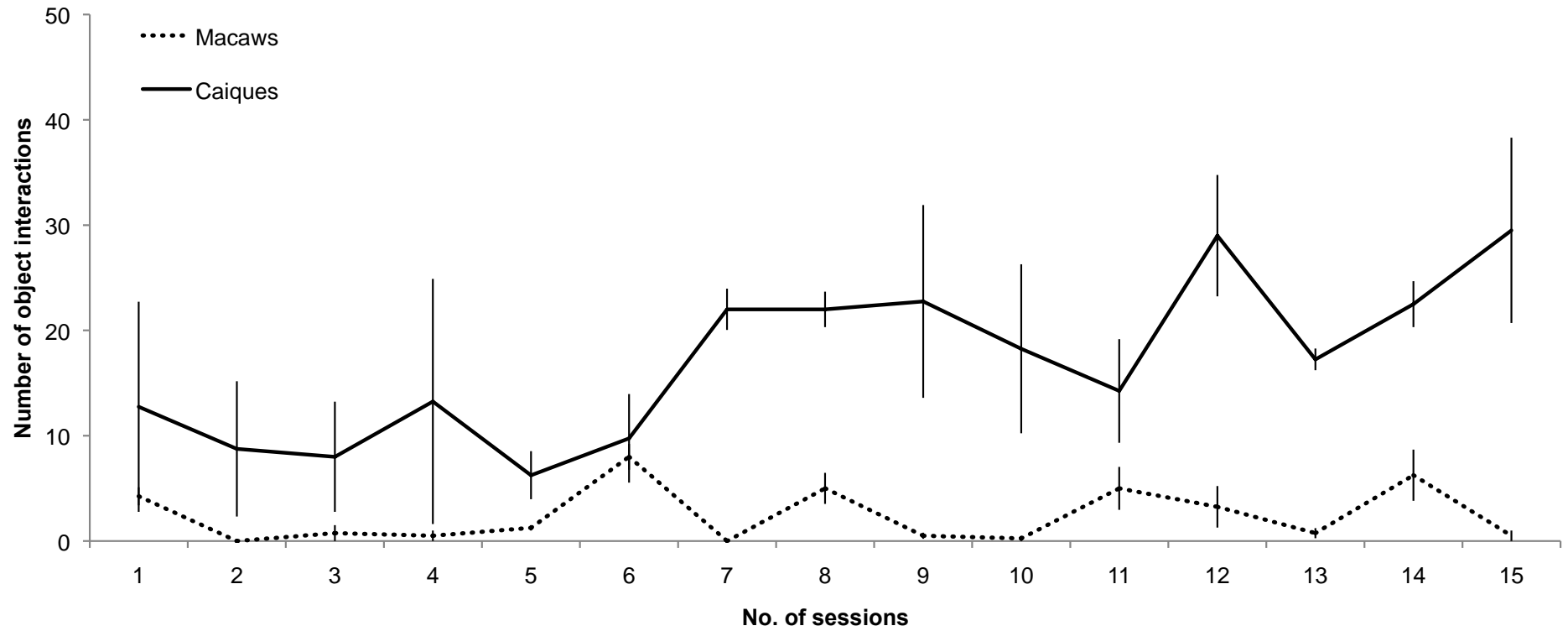


Figure 3.8a: Mean (\pm SEM) number of solitary item interactions (Y-axis) across 15 x 30min trials for Macaws and Caiques. Observations were recorded for 15 consecutive sessions after the onset of object exploration.

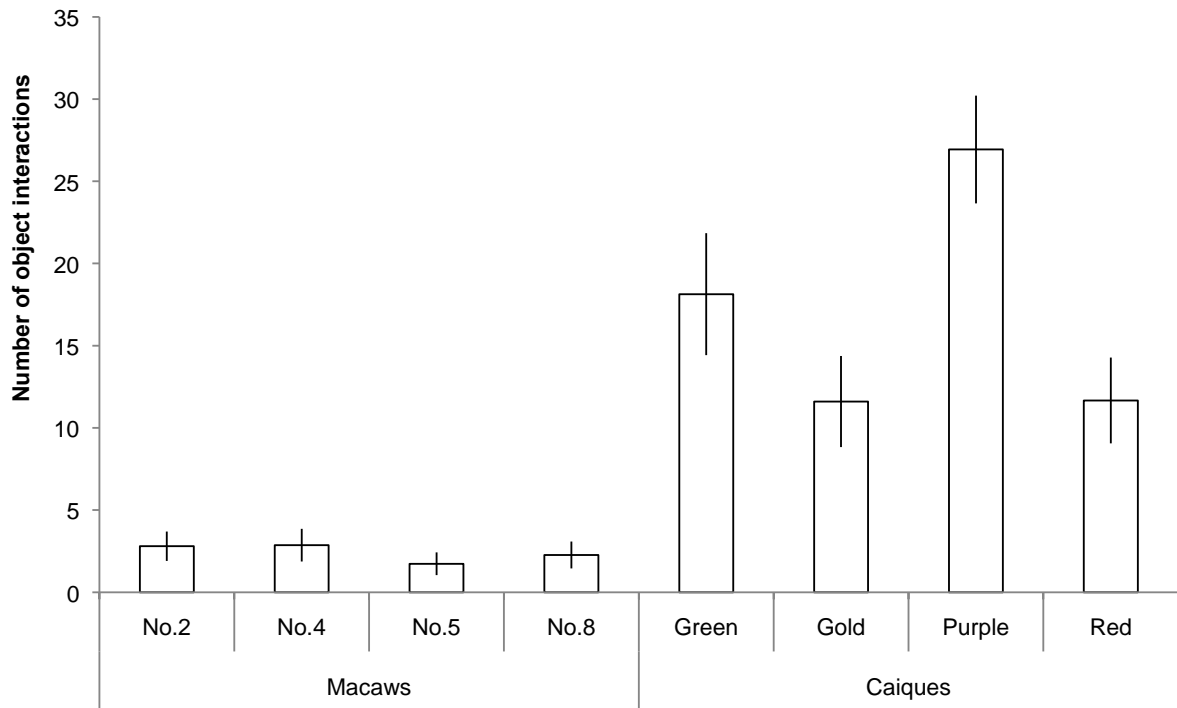


Figure 3.8b: Mean (\pm SEM) number of solitary object interactions per session for Macaws and Caiques.

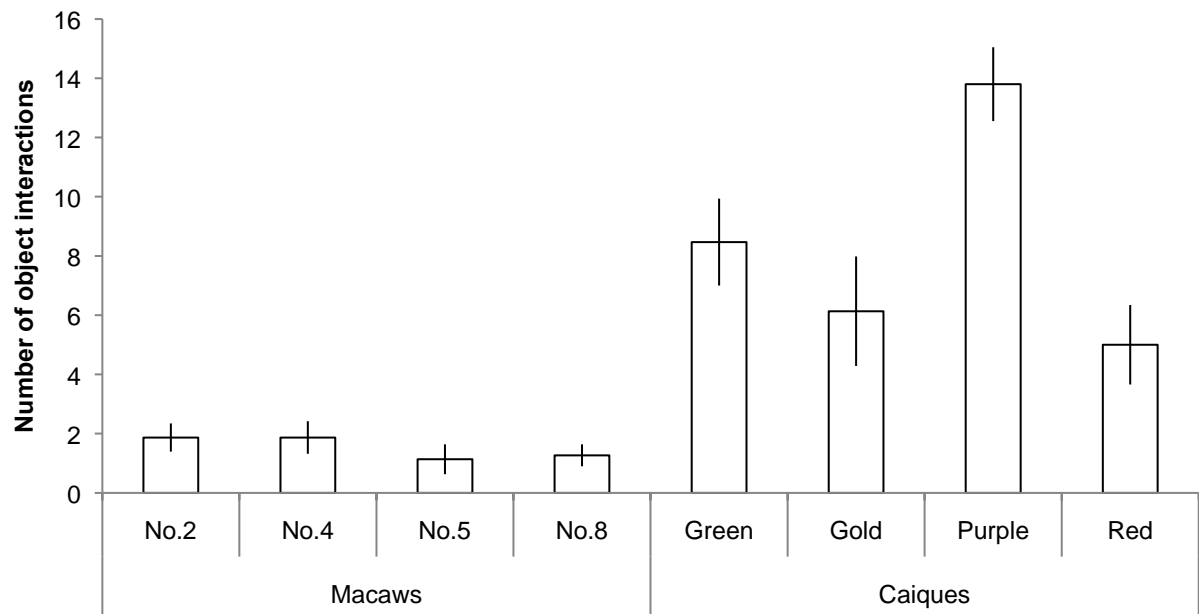


Figure 3.9a: Mean (\pm SEM) diversity of objects that were interacted with per session for Macaws and Caiques.

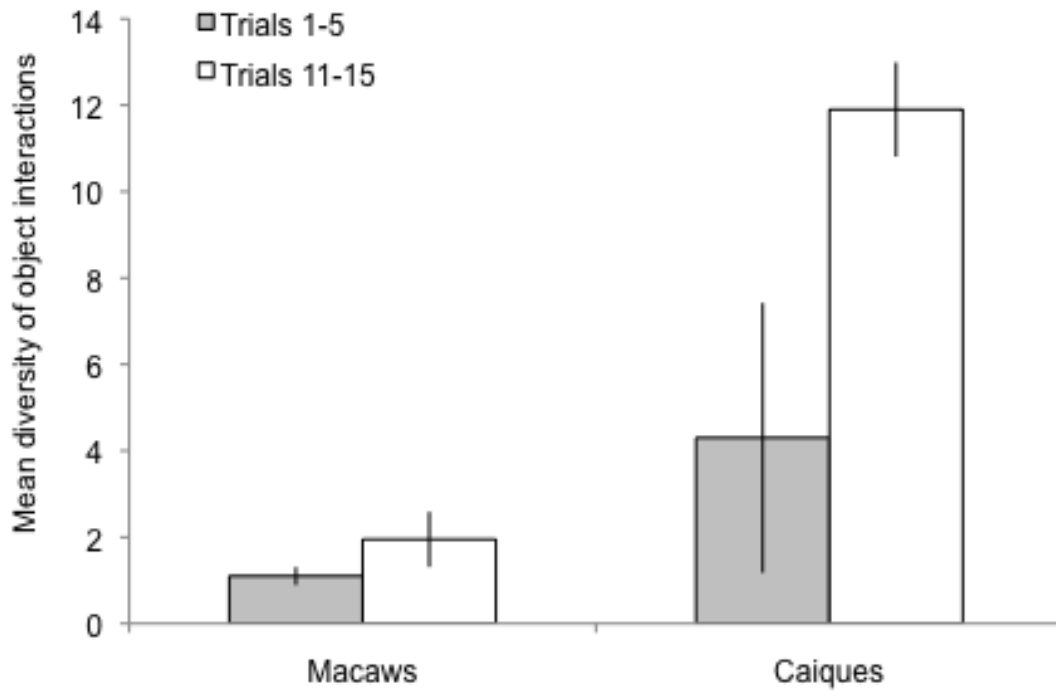


Figure 3.9b: Mean (\pm SEM) diversity of object interactions averaged across the first and last five sessions.

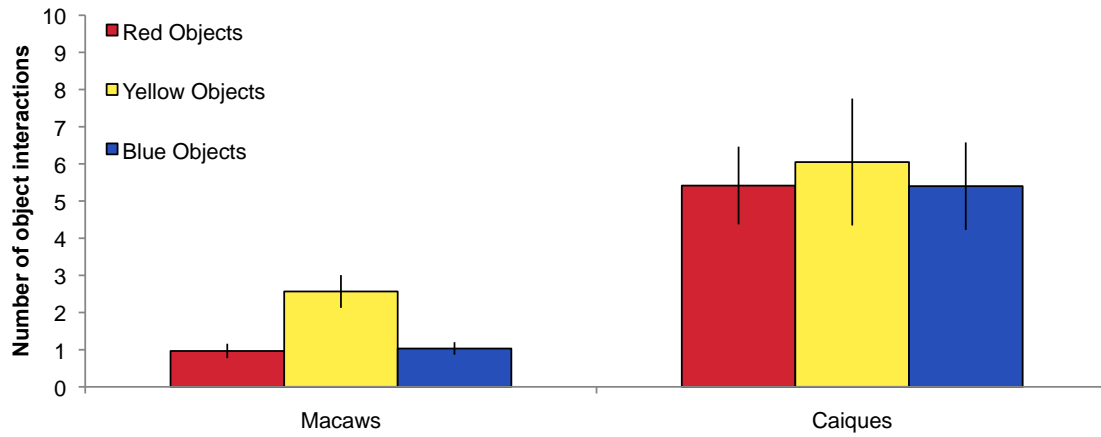


Figure 3.10: Mean (\pm SEM) number of coloured items that were explored per session for Macaws and Caiques.

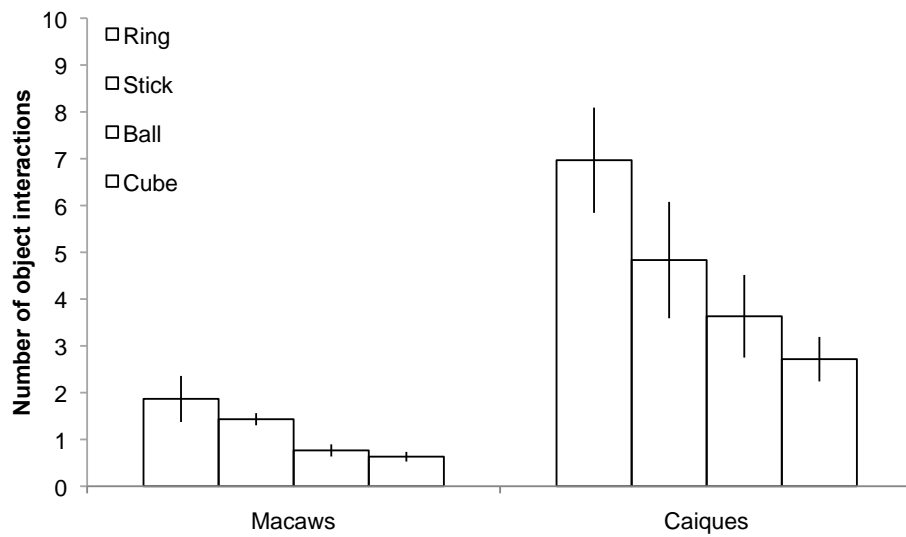


Figure 3.11: Mean (\pm SEM) number of different shapes of items that were explored per session for Macaws and Caiques.

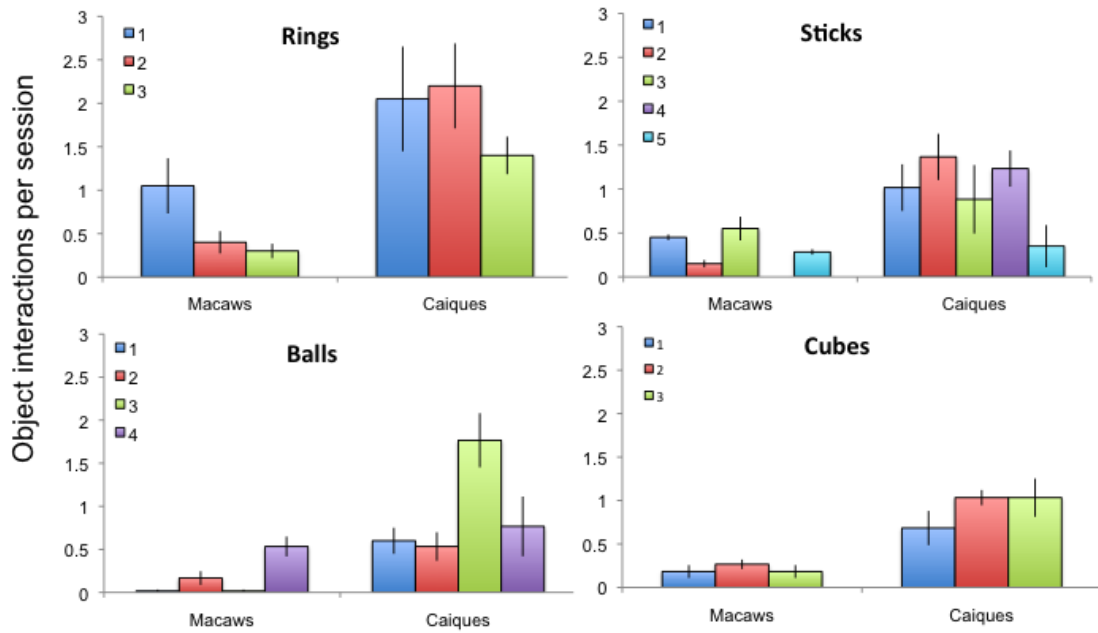


Figure 3.12: Mean (\pm SEM) overall frequencies of object interactions for the different sizes of items that were explored each session for Macaws and Caiques (size: 1 = largest, 5 = smallest).

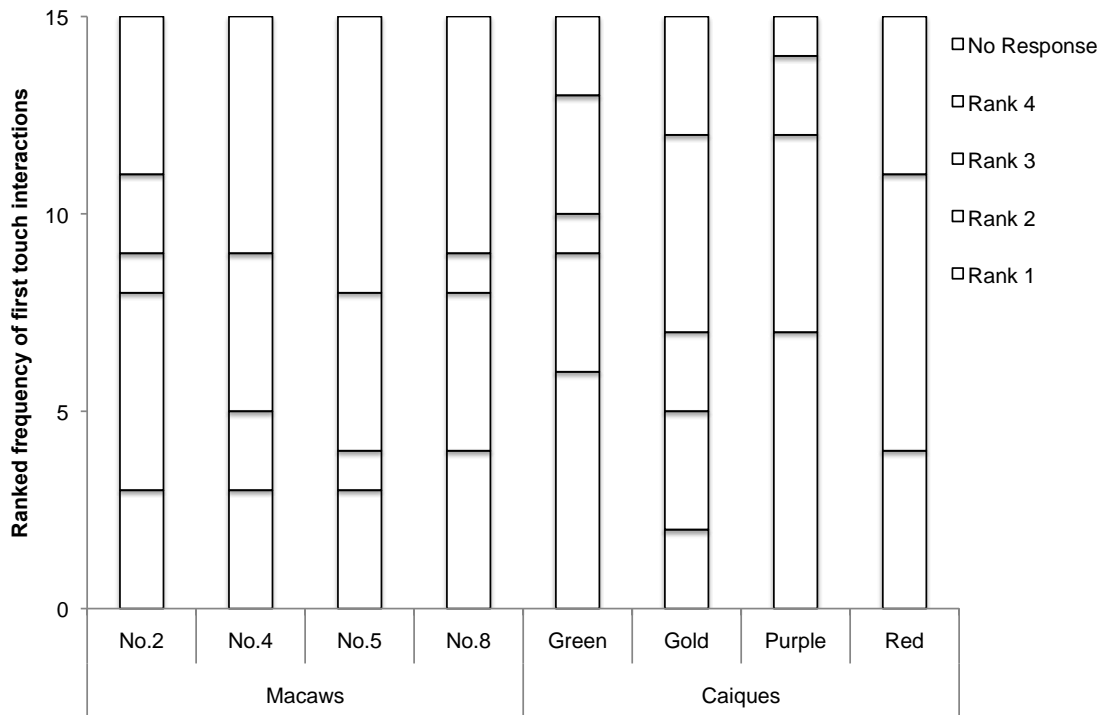


Figure 3.13: The ranked frequency of first touch interactions for each individual for 15 sessions. Rank 1 shows the number of sessions where subjects were the first in their group to touch an object. Rank 4 shows the number of sessions where subjects were the last in their group to touch an object.

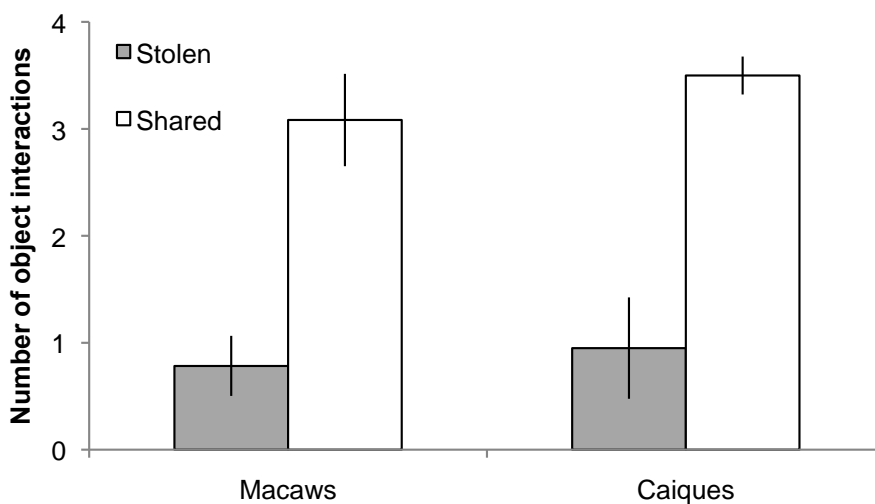


Figure 3.14a: Mean (\pm SEM) number of social object interactions per 30-minute session

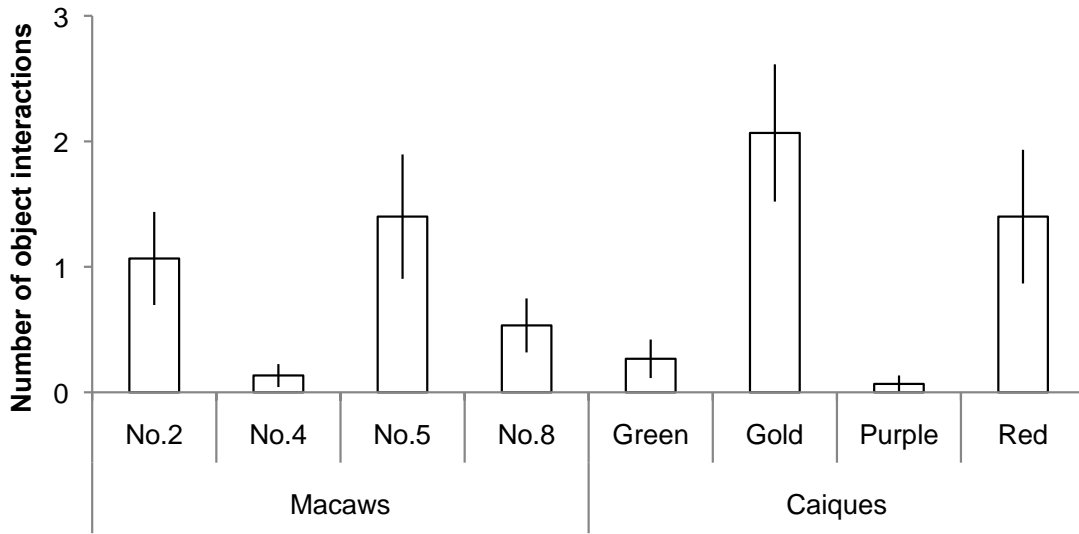


Figure 3.14b: Mean (\pm SEM) number of instigated object interactions in which an object was stolen from a conspecific (negative)

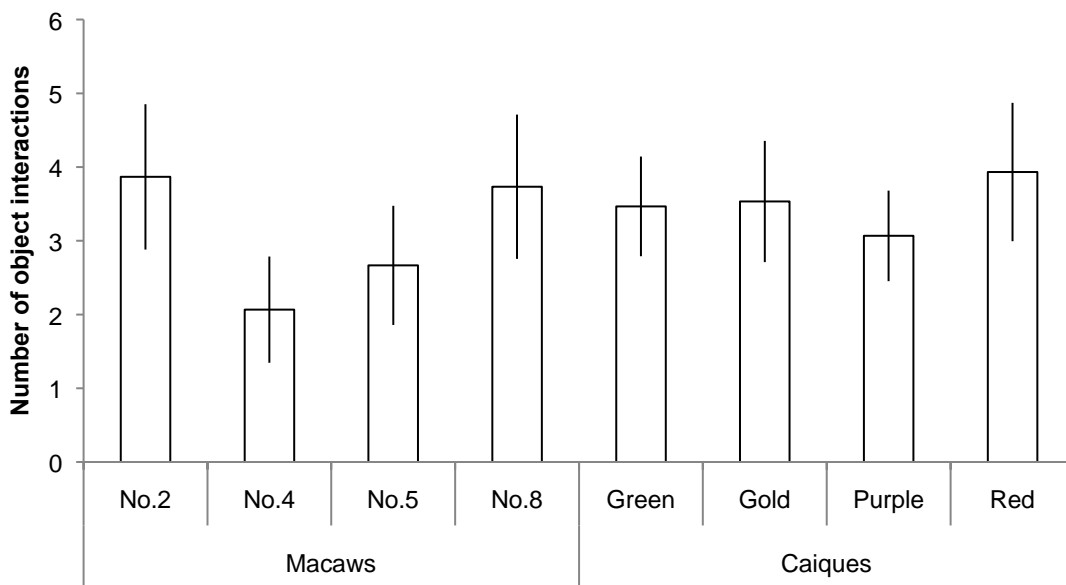


Figure 3.14c: Mean (\pm SEM) number of instigated object interactions in which an object was shared with a conspecific (positive)

3.2.4: Discussion

In this study, pronounced between-species differences in the frequency and diversity of object interactions were revealed. Caiques required fewer sessions than macaws to first explore objects and also explored a greater number, and diversity of objects than macaws.

In contrast to caiques, macaws showed relatively limited object exploration throughout the 15 observational sessions. While caiques showed a general non-significant trend to interact with a greater number of objects in later, rather than earlier, sessions, caiques interacted with a significantly greater diversity of objects in latter sessions. Macaws not only interacted with a restricted diversity of objects, but they also appeared to direct the majority of their interactions towards objects of particular colours; however these results failed to reach statistical significance. While the colour of an object may have little relevance to its functional properties, i.e. how it can be held or manipulated, macaws were more frequently observed to interact with yellow objects than objects of other colours. Macaws may therefore seek out yellow as a preferred colour. However such colour “preferences” are more likely to reflect the conservative exploratory behaviours of macaws. Hence, an initial decision to interact with yellow objects may have arisen haphazardly, but persisted as yellow became more familiar than other colours. Caiques, on the other hand, showed more generalised exploratory behaviours and interacted with all colours equally.

Both species also appeared to show preferences to manipulate certain shapes and sizes of objects. Macaws and caiques both showed a general trend to interact with rings and sticks more frequently than balls and cubes. Rings and sticks may therefore be preferred over balls and cubes, as they are easier to grasp and manipulate due to their relatively thin dimensions. Subjects were often observed to retrieve an object from the cage floor and then transport the item, using either their bill or foot, to a perch for subsequent investigation. Hence, rings and sticks were likely to be favoured as they could

be removed from the cage floor, whereas balls and cubes may be less easy to transport.

While both species showed clear preferences for the sizes of particular objects, no consistent between or within-species size relationships were observed. Macaws appeared to prefer to interact with large rings, which may have been more conspicuous to locate than small objects. However, large rings are also likely to be more challenging to manipulate than smaller rings. Hence, macaws may prefer to investigate objects that can be easily transported to a preferred location, but which also require an advanced degree of dexterity to manipulate. Caiques, on the other hand, appeared to be particularly attracted to size 3 balls. While such preferences are difficult to interpret, it may suggest that these specific items were favoured over others because they were small enough to transport, but large enough to grasp and manipulate.

Comparisons of the orders of individuals to initiate object exploration across sessions may also reveal differences between species. For macaws, all subjects displayed similar propensities to instigate object exploration. Individual differences in the distribution of first-touch interactions for caiques, however, were more pronounced. Purple and then Green were more frequently observed to instigate object exploration, than compared to Gold or Red. All of the macaws also began exploring together during their ninth presentation of the objects. Conversely, only two caiques (Purple and then Red) approached objects during their second presentation while Gold interacted with objects on the third, and Green on his fourth presentation of objects. Together, these findings suggest that macaws may be more attentive and motivated by the exploratory behaviours of conspecifics, whereas exploratory behaviours of caiques, on the other hand, appear to be more individually oriented. Interestingly (with the exception of Red), the order of first touch object interactions corresponds with the social dominance hierarchies of each species (see Chapter 2), with low ranked individuals the first to explore objects. The two lowest ranking caiques also showed the greatest

amount of exploration. Such findings may suggest that low ranking individuals are more explorative than more dominant individuals as, out of necessity, they may search out new resources to avoid displacement from dominants that can defend more regularly distributed or clumped food sources (Thornton and Samson, 2012).

Macaws and caiques, however, show some similarities in the social aspects of their object exploration. Both species engage more in shared (positive), rather than stolen (negative), social object interactions. While the frequency of shared object interactions appear to be evenly distributed across individuals of both species, stolen object interactions appear to be instigated by more dominant individuals in caiques, but not macaws (see chapter 2). Considering that parrots generally forage in social groups, and that their diets often consist of a clumped distribution of foods, such as nuts, seeds, leaves and flowers (Juniper and Parr, 2003), parrots may generally experience little aggression or displacement from conspecifics as there may be little competition over such abundant resources. However, objects were also frequently stolen from one another, suggesting that competition and displacement for limited resources, such as nesting sites or mates, may also coincide with a hierarchal dominance structure.

While findings from this study reveal pronounced between-species differences in object exploration, it may be difficult, without comparing a greater diversity of species, to extrapolate such findings to the wild. It is possible that such differences reflect species-specific adaptations to particular foraging strategies that each species may adopt in their natural environment (Day et al., 2003, Glickman and Sroges, 1966, Mettke-Hofmann et al., 2002, Tebbich et al., 2009). However, little is known about the natural history and ecology of these species. Yet, red-shouldered macaws tend to prefer open wooded habitats and savannahs, whereas black-headed caiques are generally found in closed canopy forest (Juniper and Parr, 2003). The diverse exploratory behaviours of caiques, in contrast to macaws, may therefore correspond with requirements to process a greater variety of food types that

may be typically encountered within habitats characterised by a dense and diverse closed jungle canopy. The exploratory behaviour of caiques may therefore appear typical of dietary generalists. Alternatively, the limited extent of object exploration observed in macaws may suggest that macaws possess a relatively more specialised foraging repertoire.

3.3: General Discussion

Findings from these experiments reveal striking differences in the propensities of macaws and caiques to interact with objects. When presented with a series of novel objects, while individually isolated, macaws showed relatively high levels of object neophobia in comparison to caiques. While subsequent exposure to novelty resulted in higher levels of neophobia in macaws, there was some indication that caiques habituated to novelty. Similar findings were also observed when subjects were repeatedly presented with a variety of familiar objects in a group setting. Caiques began interacting with familiar objects earlier than macaws, a likely reflection of their relatively low levels of object neophobia. Caiques also interacted with familiar objects more frequently than macaws and explored a greater diversity of objects than macaws. Subsequent exposure to these objects did not facilitate exploration in macaws, suggesting that their interactions were not inhibited by neophobia but instead reflected their naturally low propensities to interact with objects. By contrast, caiques interacted with a greater diversity of objects in later sessions, and also showed a general tendency towards interacting with objects more frequently in later sessions. Together, these findings suggest that propensities for object exploration differ substantially between these two species, which might reflect differences in their natural foraging repertoires and habitats.

In a comparative study on a variety of captive animals, Glickman and Sroges (1966) observed that certain species were more explorative of objects than

others. The authors attributed this variation to certain environmental factors that species experience in their natural habitat, such as the need to actively search for food, and avoid danger from predators. Hence, the extent of object manipulation was a likely result of adaptive selection pressures that each species experienced in their particular habitats (Glickman and Sroges 1966). Similar conclusions have been made to account for between-species differences in object neophobia. Mettke-Hofmann and colleagues (2002) found that species of parrots which inhabit relatively stable environments are more neophobic and less explorative than those species that inhabit more complex, variable environments. As such, highly neophobic species were considered to have a relatively more specialised diet than species that inhabit more diverse and variable environments. The adaptive value of neophobia was therefore considered to conserve foraging specialisations and as a result, enhance foraging efficiency (Mettke-Hofmann et al., 2002).

Little is known about the natural foraging behaviours of red-shouldered macaws and black-headed caiques, yet differences in their propensities to interact with objects may allow certain predictions, in support of previous findings from earlier studies. High levels of object neophobia, coupled with low exploration of familiar objects may suggest that macaws have a more specialised diet than caiques. Morphological evidence may also support such claims, as macaws possess a large beak that is particularly suitable for cracking open hard-cased nuts. Conversely, caiques demonstrated relatively low levels of object neophobia and were also highly explorative of familiar objects. Such findings suggest that caiques may have a more generalised diet, as their highly explorative behaviours may be a necessary adaptation to process a variety of different food types. Caiques also possess a more generic bill that appears better adapted for more generalised foraging techniques, such as prying, ripping and scraping open food items that are embedded in bark or other substrates.

Enhanced object exploration may also provide species with more experience of object relationships and therefore promote an advanced understanding of

the physical properties of objects. However, there is mixed support for such claims. While non tool-using primates (Hauser et al., 2002b), and corvids (Bird and Emery, 2009a) may demonstrate an advanced understanding of object relationships, tool naïve primates, that do not naturally use tools, have also been observed to show no appreciation for the physical properties of tools (Spaulding and Hauser, 2005).

Generalised foraging behaviours or different propensities to interact with objects may also promote differences in innovative foraging rates. Generalist species have been observed to show low neophobia and are more likely to approach and interact with novel food sources (Webster and Lefebvre, 2000). Species dependent on manipulative and explorative foraging have also been found to be more innovative than specialists (Day et al., 2003). Although rates of foraging innovations correspond positively with brain size in birds (Lefebvre et al., 1997) and primates (Reader and Laland, 2002), it is unclear whether innovative behaviours should differ between species that possess a comparable brain size but have contrasting propensities to interact with objects. The following chapters attempt to address some of these issues.

Chapter 4: Innovative Foraging

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4.1: Abstract

Propensities for innovative foraging behaviours correlate positively with brain size in birds and mammals, but are typically constrained by high neophobia and low rates of object exploration. Innovative problem solving behaviours between two species of parrots with a similar relative brain size, but which contrast in their intrinsic levels of attraction towards objects, were therefore assessed. Neophobic red-shouldered macaws and explorative black-headed caiques were individually presented with four innovative foraging tasks. Each task required subjects to inhibit non-functional actions directed towards a clearly visible food reward that was rendered inaccessible by a Plexiglas barrier. Instead, subjects were required to manipulate functional peripheral components of each task to retrieve the reward. The location of subjects' initial interactions with each apparatus, as well as the durations and counts of functional and non-functional manipulations required to obtain the rewards were assessed. All birds from both species solved each task, demonstrating comparable performances. Both species directed the majority of their behaviours towards functional, rather than non-functional, components of the tasks. Subjects however showed no initial preferences for functional components. These findings suggest that subjects learned to inhibit ineffective prepotent responses towards the food rewards, although they did not appear to extract general rules that may have allowed them to solve subsequent tasks more efficiently. Overall, red-shouldered macaws and black-headed caiques share broad propensities for innovative problem-solving behaviours, irrespective of their intrinsic differences in neophobia and object exploration.

4.2: Introduction

Innovations arise from the invention and modification of individually generated behaviours (Ramsey et al., 2007, Reader and Laland, 2003). That is, innovative behaviours may include the exploitation of a novel resource or food, the development of a new food-processing technique, use of an established behaviour in a novel context, or learning to use novel tools or technologies (Reader and Laland, 2003). As such, the capacity to produce innovative behaviours may provide a selective advantage to individuals by enhancing their foraging efficiency (Byrne, 1997), and in turn be introduced into a population's behavioural repertoire through social learning (Laland, 2004). Consequently, behavioural innovations are considered to have broad socio-ecological and evolutionary implications, particularly relevant to animal culture (Whiten et al., 1999), cognition (Reader and Laland, 2003), and species richness (Nicolakakis et al., 2003).

Rates of innovative behaviours, the taxonomic distribution of tool use, and interspecific differences in social learning, have therefore been found to correspond positively with brain size in birds and primates; as revealed from anecdotal records of novel behaviours regressed against brain size and controlled for phylogeny and research effort (Lefebvre et al., 1997, 2004, Reader and Laland, 2001, 2002). Foraging innovations and brain size also correspond positively with the successful invasion of novel habitats in birds (Sol et al., 2005), and mammals (Sol et al., 2008), as well as with an ability to tolerate climatically unstable habitats, both on a temporal and spatial scale among Neotropical parrots (Schuck-Paim et al., 2008), and British birds (Shultz et al., 2005). Together, these findings suggest that large brains allow animals to better respond to unpredictable variation in their environment, by flexibly adapting their foraging repertoires to suit locally available foods and by exploiting novel resources through innovative techniques.

While such findings may reveal broad-based between-species relationships, individual propensities for innovative behaviours are also likely to be influenced by a number of environmental or psychological processes, such as

attraction to, and avoidance of, novelty (neophilia and neophobia respectively), the necessity to innovate, and the perseverance of object exploration (Reader and Laland, 2003). Yet the mechanisms that underlie variation in innovative behaviours remain unclear (Thornton and Samson, 2012), and hence require further investigation. Neophobia and low rates of object exploration are adaptive traits that may be particularly pronounced in species that inhabit environments that require little manipulation to obtain sufficient resources (Glickman and Sroges, 1966, Mettke-Hofmann et al., 2002). Hence, a negative relationship between neophobia and innovative foraging behaviours has been observed across a range of species, including monkeys (Day et al., 2003), birds (Bouchard et al., 2007, Seferta et al., 2001, Webster and Lefebvre, 2001, 2000) and hyenas, *Crocuta crocuta* (Benson-Amram and Holekamp, 2012). However, neophobia is also a widespread trait, occurring across many species of mammals and birds (Corey, 1978, Greenberg, 2003) and can even vary considerably between different populations of the same species (Martin and Fitzgerald, 2005). Such prevalence suggests that neophobia serves a general ecological function, which is genetically determined and subject to natural selection (Bolivar and Flaherty, 2004, Minvielle et al., 2002). Most notably, neophobia appears to be linked with the plasticity of species' foraging ecologies (Greenberg, 2003). Generalist species of warblers and sparrows, for example, are less neophobic than congeneric specialists (Greenberg, 1983, 1984, 1990). Likewise, migratory garden warblers (*Sylvia borin*) are faster, and more likely to explore a novel environment than resident Sardinian warblers, *Sylvia melanocephala* (Mettke-Hofmann et al., 2009). Mettke-Hoffman and colleagues (2002) also found that parrots, which inhabit stable, predictable habitats, such as open savannahs, were more neophobic than species that inhabit more diverse and variable environments. Hence, ephemerally distributed resources may impose selection pressures that favour the exploration of novelty, whereas such behaviours may be unrewarded in more stable environments. Intra and inter-specific differences in neophobia may therefore impede innovative behaviours irrespective of brain size (Greenberg, 2003).

Reliable access to resources may also vary consistently among individuals that forage within social groups. For instance, dominant individuals may regularly gain priority access to resources by displacing subordinates. Resource acquisition may therefore be relatively stable for dominants, whereas subordinates may experience greater fluctuations in food availability. Hence, in species such as great tits (*Parus major*), individual differences in exploratory behaviours have been found to be consistent across multiple tasks and time periods (Cole and Quinn, 2012, Cole et al., 2011, Dingemanse et al., 2002, Morand-Ferron et al., 2011b, Verbeek et al., 1994), and heritable (Dingemanse et al., 2002, Drent et al., 2003). Moreover, Cole and Quinn (2012) found, in male great tits, that competitive ability—the ability to displace conspecifics from a localised food source—corresponds positively with exploration behaviour; measured as the number of hops, the number and duration of flights, and the areas visited, in a novel room. However, a negative relationship, irrespective of sex, was observed between competitive ability and problem solving performance; considered as the ability to remove a lever to access a food reward from a Perspex tube. Likewise, competitive ability has been observed to be inversely correlated with foraging innovations in male, but not female fish (Laland and Reader, 1999b). Hence, subordinates that are unable to outcompete dominants may be more likely to expose themselves to risks, such as potentially wasted time and energy, predation, or the consumption of hazardous foods, that may be associated with approaching and interacting with novel objects (Reader and Laland, 2003). As such, through necessity, young or low-ranking individuals often show high innovatory propensities and attraction towards novelty; as observed in fish (Laland and Reader, 1999a, 1999b), birds (Biondi et al., 2010, Cole and Quinn, 2012, Katzir, 1982, 1983, Morand-Ferron et al., 2011a), meerkats, *Suricata suricatta* (Thornton and Samson, 2012), hyenas, *C. crocuta* (Benson-Amram and Holekamp, 2012), and chimpanzees, *Pan troglodytes* (Reader and Laland, 2001). However, conflicting results have also been reported for some species of birds (Boogert et al., 2006, Bouchard et al., 2007, Gajdon et al., 2006) and primates (Kendal et al., 2005, Reader and Laland, 2001), suggesting that problem-solving efficiency may also improve with experience. For instance, when presented with a series of novel

extractive foraging tasks, adult callitrichid monkeys produced more successful than unsuccessful task manipulations, whereas the inverse was observed in younger individuals (Kendal et al., 2005). The intensity of individual explorative behaviours have therefore been considered as personality traits that correspond with alternative behavioural strategies (Cole and Quinn, 2012). While social status may influence an individual's necessity to innovate, such behaviours are likely to become refined through selection pressures that favour efficient foraging behaviours, which may, in turn, also result in enhanced reproductive fitness (Cole et al., 2012). Comparisons of problem-solving behaviours among individuals with established social hierarchies may therefore provide important insights to the psychological mechanisms responsible for driving individual differences in innovative behaviours.

The perseverance of object exploration may also influence whether innovative behaviours develop and become incorporated into an individual's foraging repertoire. Object exploration may allow animals to gather useful information, through trial and error learning, about the affordances of novel stimuli (Heinrich, 1995b). However, animals that continue to persevere on a task, irrespective of whether or not their behaviours result in positive feedback, may, at times, haphazardly solve a problem. Hence, solutions to problems may also be revealed through persistence of exploration, which may therefore play a key role in solving novel tasks (Thornton and Samson, 2012). Persistence of object exploration may also be linked to developmental experiences and current motivational states. Exposure to enriched rather than impoverished environments, for instance, promotes more complex and diverse exploration of novel objects in rats, *Rattus norvegicus* (Renner, 1987), enhanced problem-solving abilities in primates (Schneider et al., 1991), and low neophobia in parrots (Fox and Millam, 2007, Meehan and Mench, 2002).

In this study, the behavioural innovations of two species of parrots that contrast in their intrinsic motivation to interact with objects were assessed. Parrots are a particularly relevant family for investigating such behaviours due to their large relative brain size and propensities for innovative behaviours. Findings from previous studies suggest that macaws, in contrast to caiques,

show high levels of neophobia (Chapter 3.1) and relatively low propensities for object exploration (Chapter 3.2). Consequently, if low neophobia and high object exploration are responsible for driving innovative behaviours, we may predict caiques to solve innovative foraging tasks faster, and make more functional rather than non-functional manipulations than macaws. Subjects were individually presented with four innovative foraging tasks. Each task contained an indirectly accessible food reward that was clearly visible but positioned behind a Perspex barrier. To retrieve the reward, subjects had to inhibit direct, non-functional actions towards the reward and instead manipulate functional, peripheral components of each apparatus. As a measure of perseverance, the duration and frequencies of functional and non-functional manipulations were recorded for both species until each task was solved.

4.3: Methods

Subjects and Housing

Subjects were approximately 1.5 years old when tested. None of the subjects had prior experience with innovative problem-solving tasks.

Apparatus

Subjects were presented with one of four novel innovative foraging tasks in the following order (Figure 4.1): (1) Petri Lid; a green plastic lid with a white base, covered by a transparent petri dish lid (\varnothing 9cm x 1cm), (2) Jam Jar; a transparent glass jar with blue tissue paper covering its opening (\varnothing 8cm x 7cm high), (3) String Pulling; a transparent Plexiglas rectangular 'tube' with one end open and the other end closed, containing an item of food attached to a string which was tied to a perch 15cm above the apparatus (20cm x 3cm x 3cm), and (4) Extraction Tube; a transparent vinyl tube with blue tissue stuffed into both ends, (\varnothing 2.5cm x 7cm long). Each apparatus contained a

preferred food reward (Lafeber Nutri-Berry) that was clearly visible. To retrieve the reward, subjects were required to inhibit any actions directed towards the reward and instead manipulate peripheral components of the apparatus.

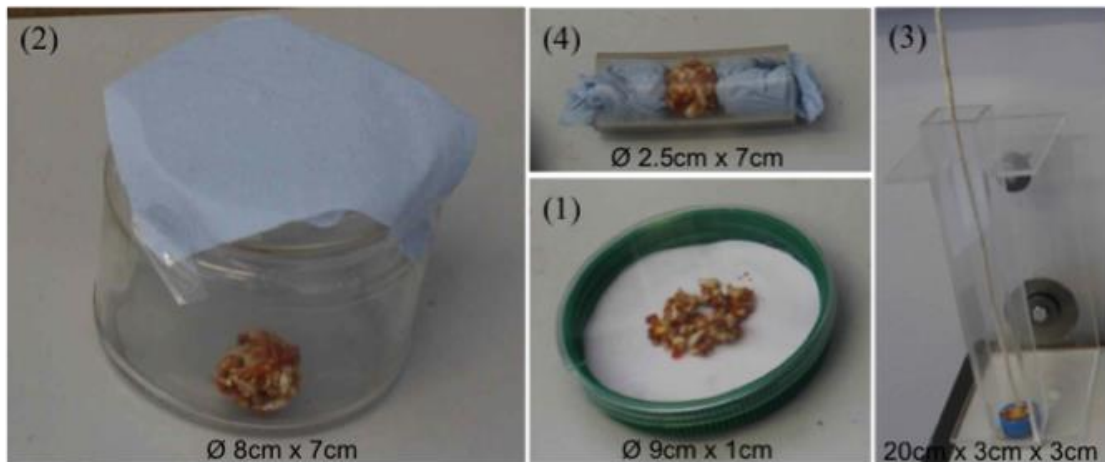


Figure 4.1: Innovative foraging tasks: (1) Petri Lid (2) Jam Jar (3) String Pulling (4) Extraction Tube.

Procedure

Subjects were transferred and tested individually in a visually isolated but familiar enclosure. Subjects were presented with each of the above tasks, in the above order. Each subject was presented with one 30 min session per day prior to their daily feeding schedule. During trials where subjects showed little motivation to retrieve rewards, the experimenter attempted to engage the subject's attention by tapping his fingers on various parts, such as the Plexiglas face (in Task 1) or glass wall (in Task 2) of an apparatus. However, during this procedure the experimenter revealed no clues as to how the task could be solved. Subjects were presented with one task per session and were required to solve each task before proceeding to the next. All trials were recorded on a digital camcorder for subsequent analysis (JVC Everio, Model No. GZ-MG645BEK, Malaysia).

Durations and frequencies of functional and non-functional manipulations required to obtain the rewards from each apparatus were recorded for each individual. The location of each subject's first-touch interactions with each apparatus were also recorded to determine whether initial interactions were directed towards functional or non-functional components. Functional manipulations involved an exploration of peripheral components related to the procurement of the reward. Non-functional manipulations involved actions directed towards the visible reward (i.e. pecking through glass or Perspex). For instance in Task 1 (Petri Lid), subjects' attempts to lever the Petri lid off the green lid were considered functional, whereas attempts to peck directly at the food in the centre of the apparatus were considered non-functional. Interactions involving manipulations of less than one second in duration, such as pecks, were coded as one second. The duration and type of each subject's manipulations for all four tasks were video recorded for subsequent analysis.

Statistical Analysis

Data were assessed with Shapiro-Wilk and Levene's tests and were log transformed to meet assumptions of normality and homogeneity of variance for parametric analysis. Because some values comprised of zeros or ones, a value of 10 was added to each data point prior to transformation. Comparisons of log-transformed durations (seconds) of functional and non-functional manipulations were made using Repeated Measures ANOVA. Log-transformed counts of functional and non-functional manipulations were also assessed using Repeated Measures ANOVA. Planned post-hoc tests were not corrected for multiple pairwise comparisons, and were made using paired t-tests. The location of first touch manipulations (either functional or non-functional) failed to meet assumptions of normality. Counts of functional and non-functional first touch locations were therefore summed across individuals and within subjects comparisons were made with a non-parametric Wilcoxon-Signed Ranks test. Exact tests were reported for non-parametric analyses, following the procedures outlined by Mundry and Fischer (1998). All data were assessed in SPSS (SPSS for Mac OS X, 2007).

4.4: Results

Durations of functional and non-functional manipulations

All individuals from both species eventually solved each of the four innovative foraging tasks. There were however no significant between-species differences in the log-transformed durations of time required to solve each problem (macaws: mean = 2.90 ± 0.11 SEM; caiques: mean = 3.11 ± 0.04 SEM; Table 4.1; Figure 4.2); Repeated measures ANOVA, $F_{1,6} = 3.225$, $p = 0.123$. There was no significant within subjects effect of task (Task 1: mean = 2.86 ± 0.16 SEM; Task 2: mean = 2.68 ± 0.12 SEM; Task 3: mean = 3.32 ± 0.30 SEM; Task 4: mean = 3.17 ± 0.23 SEM); Repeated measures ANOVA, $F_{3,18} = 1.425$, $p = 0.268$, and no significant task x species interaction; Repeated measures ANOVA, $F_{3,18} = 0.527$, $p = 0.669$, suggesting that each task required similar amounts of time to solve and that both species performances were similar across tasks.

A significant within subjects effect of manipulation type (functional: mean = 1.57 ± 0.04 ; non-functional: mean = 1.29 ± 0.03 ; Figure 4.3); Repeated measures ANOVA, $F_{1,6} = 51.512$, $p < 0.001$, and no significant manipulation type x species interaction; Repeated measures ANOVA, $F_{1,6} = 0.034$, $p = 0.859$, suggests that both species directed greater attention towards making functional, rather than non-functional, manipulations.

A significant task x manipulation type interaction was however observed (Figure 4.4); Repeated measures ANOVA, $F_{3,18} = 5.113$, $p = 0.01$, suggesting that the amount of time spent making functional and non-functional manipulations differed for some tasks but not others. Planned, uncorrected post-hoc tests revealed that subjects spent significantly more time making functional manipulations for: Task 2 (functional: mean = 1.55 ± 0.07 SEM; non-functional: mean = 1.13 ± 0.06 SEM); paired t-test, $t = 6.786$, $df = 7$, $p < 0.001$; Task 3 (functional: mean = 1.78 ± 0.15 SEM; non-functional: mean = 1.53 ± 0.17 SEM); paired t-test, $t = 2.687$, $df = 7$, $p = 0.031$; and Task 4 (functional: mean = 1.82 ± 0.13 SEM; non-functional: mean = 1.35 ± 0.13

SEM); paired t-test, $t = 4.671$, $df = 7$, $p = 0.002$; but not for Task 1 (functional: mean = 1.43 ± 0.10 SEM; non-functional: mean = 1.43 ± 0.08 SEM); paired t-test, $t = 0.075$, $df = 7$, $p = 0.943$.

Counts of functional and non-functional manipulations

There were no significant between-species differences in the number of functional or non-functional manipulations (macaws: functional mean = 1.29 ± 0.04 SEM; non-functional mean = 1.21 ± 0.06 SEM; caiques: functional mean = 1.26 ± 0.08 SEM; non-functional mean = 1.22 ± 0.05 SEM); Repeated measures ANOVA, $F_{1,6} = 0.029$, $p = 0.869$ (Table 4.2).

A significant within subjects effect of manipulation type (functional: mean = 1.27 ± 0.04 SEM; non-functional: mean = 1.22 ± 0.04 SEM); Repeated measures ANOVA, $F_{1,6} = 28.743$, $p = 0.002$, and no significant within subjects manipulation type x species interaction; Repeated measures ANOVA, $F_{1,6} = 4.588$, $p = 0.076$, suggests that both species made more functional, rather than non-functional manipulations.

There was no significant within subjects effect of task (Task 1: mean = 2.48 ± 0.13 SEM; Task 2: mean = 2.25 ± 0.07 SEM; Task 3: mean = 2.61 ± 0.21 SEM; Task 4: mean = 2.62 ± 0.10 SEM); Repeated measures ANOVA, $F_{3,18} = 1.259$, $p = 0.318$, and no significant within subjects task x species interaction; Repeated measures ANOVA, $F_{3,18} = 0.405$, $p = 0.751$, suggesting that each task required a similar number of manipulations to solve, and that species performances were equivalent across tasks.

A significant within subjects task x manipulation type interaction was however revealed (Figure 4.5); Repeated measures ANOVA, $F_{4,24} = 5.952$, $p = 0.005$, suggesting that the number of functional and non-functional manipulations were significantly different for some tasks but not others. Planned, uncorrected post-hoc tests revealed that subjects made a significantly greater number of functional manipulations for: Task 2 (functional: mean = 1.16 ± 0.04 SEM; non-functional: mean = 1.09 ± 0.03 SEM); paired t-test, $t = 2.509$,

df = 7, $p = 0.04$; and Task 4 (functional: mean = 1.41 ± 0.06 SEM; non-functional: mean = 1.21 ± 0.05 SEM); paired t-test, $t = 4.200$, df = 7, $p = 0.004$, but not for Task 1 (functional: mean = 1.21 ± 0.06 SEM; non-functional: mean = 1.26 ± 0.07 SEM); paired t-test, $t = 1.285$, df = 7, $p = 0.240$, or Task 3 (functional: mean = 1.31 ± 0.10 SEM; non-functional: mean = 1.30 ± 0.11 SEM); paired t-test, $t = 0.120$, df = 7, $p = 0.908$.

Location and type of first-touch manipulations

There were no significant within subjects differences for the number of functional versus non-functional first-touch manipulations (functional: mean = 2.25 ± 0.89 SEM; non-functional: mean = 1.75 ± 0.89 SEM; Table 4.3); Wilcoxon-Signed Ranks test, $z = 0.816$, $N - \text{Ties} = 8$, $p = 0.75$. However, one caique, Gold, made functional first touch manipulations for all four tasks.

Dominance hierarchy and duration to retrieve food

To assess whether dominance rank was associated with problem solving ability, durations to retrieve the reward between the two most dominant individuals and the two most subordinate individuals were compared (Table 2.2). No significant differences in problem solving durations were found between dominant and subordinate individuals (Dominant: mean = 3.07 ± 0.09 SEM; Subordinate: mean = 2.94 ± 0.09 SEM); independent t-test, $t = 1.05$, df = 6, $p = 0.33$ (Figure 4.2).

Table 4.1: Raw durations of functional and non-functional manipulations (sec) required to retrieve a food reward from each innovative foraging problem

	Task 1: Petri Lid		Task 2: Jam Jar		Task 3: String Pulling		Task 4: Extraction Tube	
	Functional	Non-functional	Functional	Non-functional	Functional	Non-functional	Functional	Non-functional
MACAWS								
No.2	2.00	13.00	14.00	3.00	203.00	118.00	6.00	4.00
No.4	5.00	16.00	41.00	6.00	35.00	0.00	20.00	2.00
No.5	58.00	14.00	7.00	0.00	25.00	14.00	48.00	2.00
No.8	40.00	63.00	34.00	1.00	35.00	9.00	153.00	14.00
CAIQUES								
Green	7.00	9.00	48.00	3.00	21.00	0.00	130.00	105.00
Gold	15.00	8.00	46.00	22.00	40.00	65.00	93.00	9.00
Purple	44.00	31.00	28.00	0.00	14.00	14.00	116.00	36.00
Red	10.00	7.00	13.00	1.00	319.00	162.00	36.00	2.00

Table 4.2: Raw counts of functional and non-functional manipulations required to retrieve a food reward from each innovative foraging problem

	Task 1: Petri Lid		Task 2: Jam Jar		Task 3: String Pulling		Task 4: Extraction Tube	
MACAWS	Functional	Non-functional	Functional	Non-functional	Functional	Non-functional	Functional	Non-functional
No.2	1	2	3	2	57	33	3	4
No.4	2	6	10	5	3	0	10	2
No.5	21	13	1	0	5	7	10	2
No.8	19	41	8	1	12	5	37	12
CAIQUES								
Green	2	5	5	3	1	0	18	17
Gold	5	4	8	9	6	16	21	6
Purple	10	13	2	0	2	3	29	9
Red	2	2	1	1	38	60	15	2

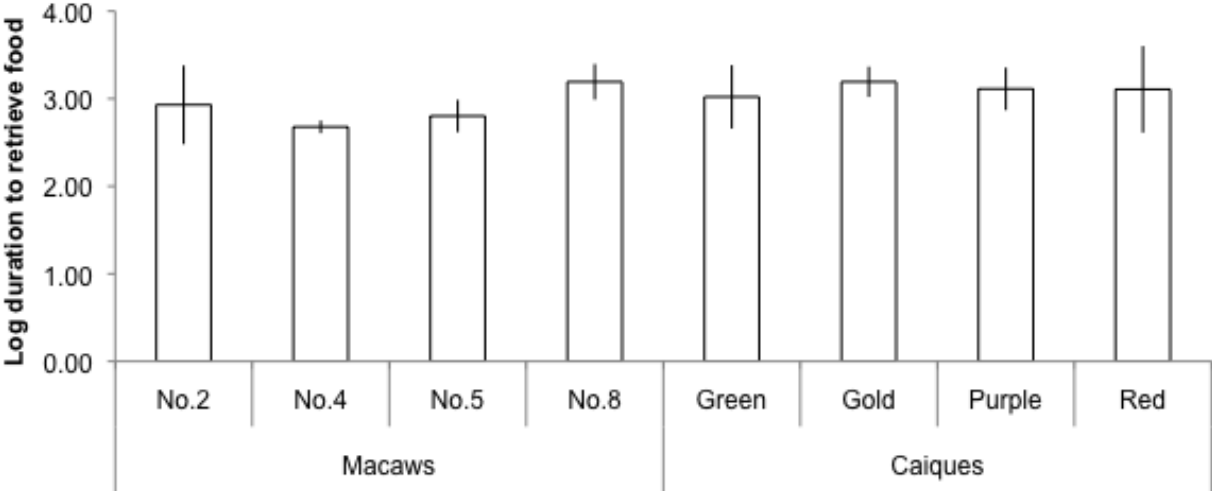


Figure 4.2: Mean log transformed durations (sec ± SEM) to solve four innovative foraging tasks for each individual.

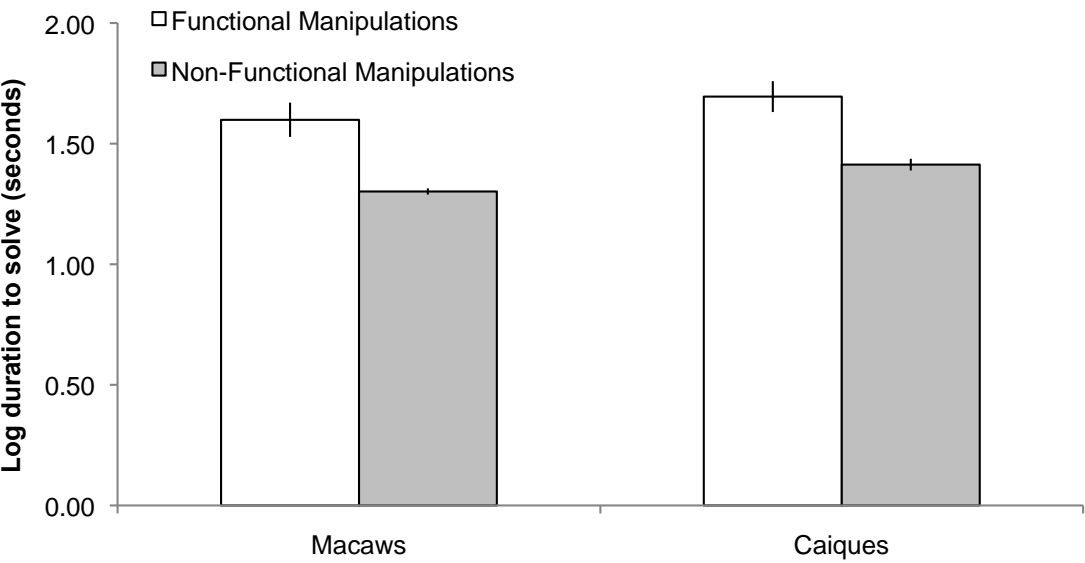


Figure 4.3: Mean log transformed durations (sec ± SEM) of functional and non-functional manipulations required to solve four innovative foraging tasks.

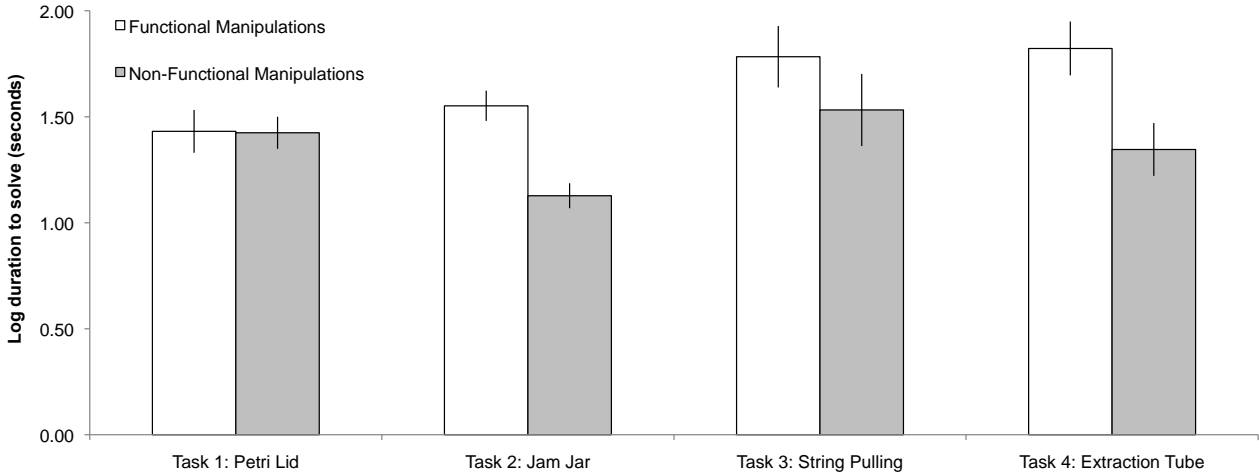


Figure 4.4: Mean log transformed durations (sec ± SEM) of functional and non-functional manipulations required to solve each innovative foraging task for pooled subjects.

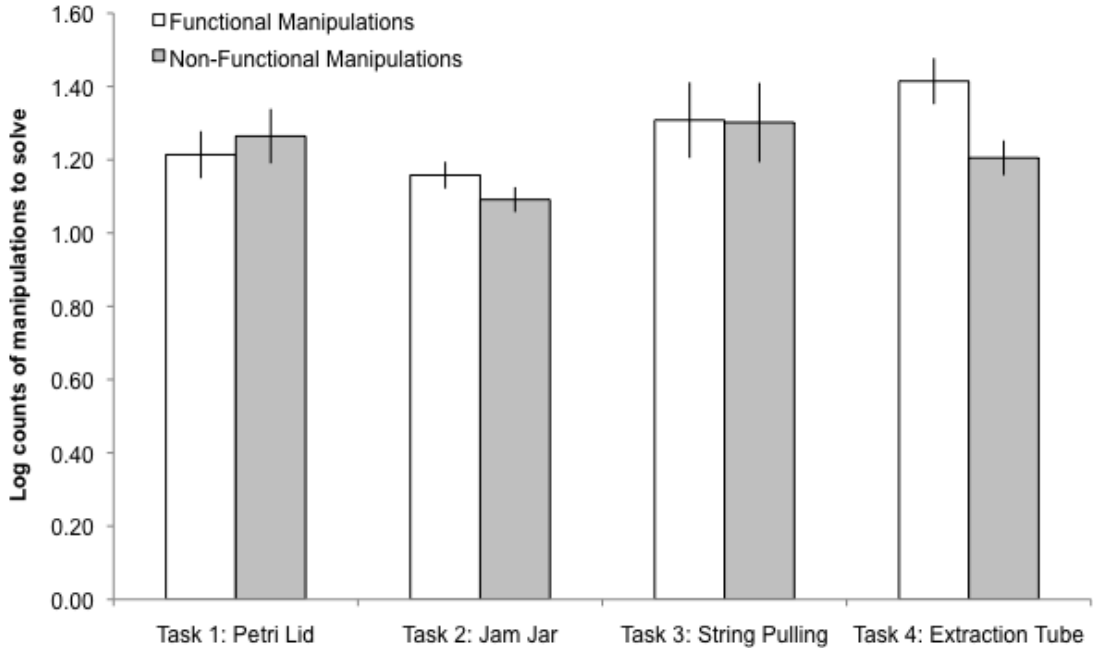


Figure 4.5: Mean log transformed counts (± SEM) of functional and non-functional manipulations required to solve each innovative foraging task for pooled subjects.

Table 4.3: Functional (Yes) and non-functional (No) locations of first touch manipulations for each task.

Task	Macaws				Caiques			
	No.2	No.4	No.5	No.8	Green	Gold	Purple	Red
(1) Petri Dish	No	No	No	No	No	Yes	No	No
(2) Jam Jar	No	Yes	Yes	Yes	Yes	Yes	Yes	No
(3) String Pulling	Yes	Yes	No	Yes	No	Yes	No	Yes
(4) Extraction Tube	No	Yes	Yes	No	No	Yes	Yes	Yes

4.5: Discussion

Results from this study reveal that red-shouldered macaws and black-headed caiques share broad propensities for innovative problem solving behaviours. All individuals from both species demonstrated comparable abilities to solve each of the four innovative foraging tasks. Although both species showed no initial preference for manipulating functional components of the tasks, subjects later directed the majority of their attention towards manipulating functional, rather than non-functional, components of each apparatus. These findings reveal that subjects not only learned the affordances associated with manipulating functional peripheral components of the tasks, but were also capable of inhibiting non-functional prepotent responses towards a clearly visible reward, suggesting inhibitory control. Furthermore, all subjects showed comparable performances at solving innovative foraging problems irrespective of differences in their hierarchical social status (Figure 4.2 & Table 2.2 respectively). The comparable performances of both species on these tasks, irrespective of their intrinsic differences to interact with objects (Chapter 3), also suggests that the intensity of neophobia and object exploration may have little overall influence on propensities for innovative foraging behaviours in species that are tested in captivity.

The high proportion of successful individuals in this study suggests that these tasks may not have been particularly difficult for these species to solve, and that macaws and caiques may be broadly capable of generating innovative behaviours to solve a variety of novel foraging problems. However, high rates of innovation are often reported in captive species in comparison to their wild counterparts, for example in primates (Reader and Laland, 2003), hyenas, *C. crocuta* (Benson-Amram et al., 2013) and a number of bird species (Bouchard et al., 2007, Gajdon et al., 2004, Morand-Ferron et al., 2011a, Webster and Lefebvre, 2001). In the wild, few individuals within a social group successfully solve innovative foraging problems. Success rates of 15% of 62 individuals have been reported for wild hyenas (*C. crocuta*), even after repeated exposure to a novel foraging task (Benson-Amram and Holekamp, 2012). Similar findings have been observed in wild vervet monkeys (*Cercopithecus aethiops*), where only 32% of 53 individuals successfully solved a novel foraging task (van de Waal and Bshary, 2010). Moreover, success rates as low as 7% of 30 individuals were reported in vervet groups that had minimal exposure to humans (van de Waal and Bshary, 2010). In a study involving 135 meerkats (*S. suricatta*), 63 individuals interacted with innovative foraging tasks, while only 13 individuals (10%) successfully retrieved the food reward (Thornton and Samson, 2012). Similar findings have also been reported for birds, where only 14% of 236 great tits (*P. major*), and blue tits (*Cyanistes caeruleus*) successfully solved an innovative foraging problem (Morand-Ferron et al., 2011a).

The relatively low number of successful innovators in the wild, in comparison to captivity, suggests that individual propensities for innovative behaviours may be mitigated by certain socio-ecological influences. Testing individuals in isolation may therefore alleviate some of the external social influences that discourage object exploration, such as enhanced competition or displacement from conspecifics. Individuals tested in isolation may therefore show greater exploratory behaviours, which may enhance their foraging success, as observed in captive hyenas in contrast to their wild counterparts (Benson-Amram et al., 2013).

In this study, both macaws and caiques revealed comparable propensities for innovative problem solving behaviours. Such findings may be expected, given that both species possess an equivalently large relative brain size (Iwaniuk et al., 2005), and a large forebrain size that corresponds positively with rates of innovative foraging behaviours in birds (Lefebvre et al., 1997). However, results from previous studies reveal that macaws are intrinsically more neophobic (Chapter 3.1) and less explorative (Chapter 3.2) of objects than caiques. While, numerous studies support an inverse relationship between innovative performances, object exploration and neophobia (Auersperg et al., 2011, Benson-Amram and Holekamp, 2012, Bouchard et al., 2007, Day et al., 2003, Greenberg, 2003, Overington et al., 2011, Reader and Laland, 2003, Seferta et al., 2001, Webster and Lefebvre, 2001), results from the current study suggest that differences in neophobia and object exploration may have little overall influence on innovative propensities per se. The intensity of neophobia may therefore diminish over time as animals become habituated, through repeated exposure, to particular novel objects or foods. As the extent of neophobia diminishes, habituation may then facilitate greater object exploration (Greenberg, 2003). Certainly, some of the most innovative taxa, such as corvids and parrots, show strong neophobic and explorative behaviours; suggesting that explorative tendencies may be adaptive when species depend on exploring new situations to survive, while neophobia may promote high levels of fear as a mechanism to conserve exploratory behaviours, and hence maintain foraging efficiency, in habitats characterised by abundant resources (Greenberg, 2003, Greenberg and Mettke-Hofmann, 2001).

Macaws and caiques both showed no initial preference for manipulating the functional components of each apparatus. Yet subjects later focused the majority of their behaviours towards manipulating functional, rather than non-functional, components. Subjects showed clear preferences for manipulating functional, rather than non-functional, components in the two tasks that involved removing tissue paper to retrieve the reward (Task 2 & Task 4; Figure 4.4 & 4.5). However, the duration and frequency of functional and non-functional manipulations were similar in Tasks 1 and 3, which did not use

tissue paper, but instead required subjects to remove a lid or pull up a string (Figure 4.4 & 4.5). Hence, subjects had difficulty in targeting, and subsequently manipulating, tasks when they were required to manipulate potentially more complex functional components. Macaws and caiques initially required experience of each apparatus before learning which of the components were functional and could therefore be manipulated to obtain a reward. Complex and novel foraging apparatuses are however likely to require initial exploration, and hence trial and error experience, before solutions to such problems may be revealed and learned through association. Similar findings have also been reported in wild hyenas, *C. crocuta* (Benson-Amram and Holekamp, 2012) and meerkats, *S. suricatta* (Thornton and Samson, 2012), where successful individuals reduced the amount of time spent manipulating non-functional components with repeated presentations of the same task. These findings also suggest that both macaws and caiques learned to inhibit non-functional prepotent actions towards the food reward through the clear Plexiglas barrier, and instead focus their efforts on manipulating functional, but peripheral, components of the tasks. Through experience, subjects could have potentially learned to immediately attend to the functional components of each novel task. However, like meerkats (Thornton and Samson, 2012), caiques and macaws did not appear to generalise these learned inhibitory behaviours across different tasks. This study not only reveals that red-shouldered macaws and black-headed caiques are broadly capable of generating innovative problem-solving behaviours, but that that intrinsic differences in neophobia and object exploration may have little overall influence on propensities for innovative foraging behaviours.

Chapter 5: Means-End Comprehension of Object Relationships

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5.0.1: Abstract

Physical cognition has traditionally been assessed in large-brained tool-using species, such as corvids and apes. Parrots, like corvids and apes, also possess a relatively large brain, yet comparable performances on physical cognition tasks are rarely reported in this group, possibly because parrots do not regularly use tools in the wild. This study was therefore designed to investigate physical comprehension of object relationships between tool-using and non tool-using species using a series of means-end tasks. In Experiment 1, the Connected problem, subjects were tested on their ability to discriminate between pulling familiar materials that were either connected to rewards, or disrupted by a gap. After reaching a significant criterion of correct choices, subjects were presented with a novel transfer task involving a functionally equivalent problem, but with unfamiliar materials. Macaws and caiques both rapidly solved the connected discrimination problem, with some birds demonstrating near spontaneous comprehension. However, success on the novel transfer task was relatively poor, suggesting that novel materials impeded their performances. In Experiment 2, the Trap-Gaps Problem, six of eight birds solved the initial task, but required extensive trial-and-error experience to learn to discriminate between pulling food-trays through gaps while attending to the respective width of the gaps and size of the trays. However, four of these six birds rapidly solved the transfer task, with one caique demonstrating spontaneous comprehension of the problem. Overall, these findings suggest that non tool-using parrots may possess capacities for sophisticated physical cognition and an ability to solve novel problems by generalising learned rules.

5.0.2: General Introduction

Although much of the research on physical cognition has traditionally focused on apes, which frequently use tools in the wild (Povinelli, 2000, Tomasello and Call, 1997), non tool-using species may also show capacities for physical cognition when tested in captivity. For example, vervet monkeys, which do not regularly use tools in the wild, have been found to outperform tool-using chimpanzees on a Trap-Table problem that requires subjects to rake in a reward while avoiding a trapping hole (Povinelli, 2000, Santos et al., 2006). Moreover, some species of corvids, which do not regularly use tools in the wild, show advanced capacities for manufacturing and using tools in captivity (Bird and Emery, 2009a, 2009b, Cheke et al., 2011, Seed et al., 2006); demonstrating performances that are comparable to frequent tool-using corvids (Taylor et al., 2009, Weir et al., 2002) and possibly apes (Hanus et al., 2011, Mendes et al., 2007).

Successful performances of species on physical cognition tasks may not necessarily correspond with whether or not an animal naturally uses tools in the wild. However, the extent to which subjects are trained on particular tasks, as well as their previous experiences on similar problems or with particular objects or materials, may vary widely between studies, and hence influence such findings. For example, when non-tool-using cotton-top tamarins were provided with training prior to testing, subjects successfully solved a variety of tasks that required some understanding of object relationships and the functionality of tools (Hauser, 1997, Hauser et al., 1999, 2002b, Santos et al., 2006). However, tool naïve cotton-top tamarins failed to solve such problems without prior training or familiarity with testing materials (Spaulding and Hauser, 2005). Similar findings have also been reported from studies on apes, which appear to be capable of solving simple object-related problems without previous exposure to the testing materials, but have difficulty solving more challenging problems when using unfamiliar, rather than familiar, materials (Herrmann et al., 2008). Comparisons between tool-using and non tool-using species that are raised under similar conditions, but subjected to

experimental differences in their pre-exposure to testing materials, may therefore reveal whether familiarity and experience of particular materials influence subjects' performances on object related tasks.

However, surprisingly few accounts of spontaneous tool-use have been reported in captive parrots, in comparison to primates or corvids, and even fewer accounts from wild populations. Hyacinth macaws (*Anodorhynchus hyacinthinus*) have been observed using wooden wedges as tools to better secure and manipulate hard cased nuts with their upper mandible, both in the wild (Schneider et al., 2002) and in captivity (Bertagnolio, 1994, Borsari and Ottoni, 2005). Similar observations have also been reported for wild palm cockatoos, *Probosciger aterrimus*, by Wallace (2000) in 1869. Perhaps the most convincing and recent account of spontaneous tool innovation in captive parrots has been described from one individual, Figaro, a Goffin's cockatoo, *Cacatua goffini*, (Auersperg et al., 2012). In this instance, Figaro used a number of techniques and materials to successfully manufacture stick tools to retrieve otherwise out-of-reach cashew nuts (Auersperg et al., 2012). Other studies on captive kea have also revealed detailed capacities for tool related behaviours (Huber and Gajdon, 2006). Although kea do not naturally use tools, they are highly inquisitive and readily adopt multiple tool-oriented techniques to access rewards; demonstrating performances that are comparable to species that regularly use tools in the wild, such as New Caledonian crows (Auersperg et al., 2011). While parrots may be infrequently challenged with the necessity to use tools in their natural environment, and hence spontaneous tool-use may be rarely observed among wild parrots, these findings suggest that some parrots may potentially possess sophisticated capacities for tool-using behaviours. As such, controlled experiments that assess tool-using behaviours among captive species of parrots may help reveal their capacities to comprehend object related problems. Classical approaches used to assess means-end reasoning, planning and insight are vertical and horizontal string-pulling problems.

Vertical String Pulling

The ability to pull up a vertically hanging string to obtain an out-of-reach reward is generally considered a cognitively complex task (Schuck-Paim et al., 2009). For birds, this task requires the sequential use of novel behavioural actions such as grasping the string with their beak, pulling it up and holding the slack with their foot. Along with the ability to monitor the string, food and body movements, these actions, if accomplished repeatedly, result in the acquisition of the food attached to the end of the string. The spontaneous accomplishment of this task has been suggested to indicate insight and planning, as well as demonstrate an appreciation for the causal properties of the string, by understanding invisible forces, such as gravity, and observable physical rules, such as connectedness, that mediate object relationships (Heinrich, 1995a, Heinrich and Bugnyar, 2005, Schuck-Paim et al., 2009). However, the sting-pulling performances of New Caledonian crows become impaired when their visual information of the approaching reward is restricted, suggesting that string-pulling behaviours may be reinforced by a perceptual-motor feedback cycle, and hence mediated by processes of operant conditioning, rather than spontaneous insight (Taylor et al., 2010).

While some species of birds, such as goldfinches (*Carduelis carduelis*) and siskins (*Carduelis spinus*) have difficulty retrieving an out-of-reach reward suspended from a string (Seibt and Wickler, 2006), other species, such as budgerigars (*Melopsittacus undulatus*) and starlings (*Acridotheres tristis*) may be capable of pulling up strings, but require extensive experience before learning to discriminate between pulling strings that are connected to a reward, rather than strings where no rewards are present (Ducker and Rensch, 1977). Some parrots and corvids, however, show an ability to spontaneously, if not rapidly, solve more complicated configurations of this task, by correctly discriminating between rewarded, rather than unrewarded crossed-strings and broken-strings (Bagotskaya et al., 2012, Heinrich, 1995a, Heinrich and Bugnyar, 2005, Krasheninnikova et al., 2013, Werdenich and

Huber, 2006), as well as discriminating between pulling strings based on the perceived effort required to retrieve a reward (Pfuhl, 2012).

Most parrots and corvids tested on string-pulling tasks efficiently solve simple problems that require no discrimination between strings, without training, and on their first trial (Bagotskaya et al., 2012, Heinrich, 1995b, Heinrich and Bugnyar, 2005, Krasheninnikova et al., 2013, Magat and Brown, 2009, Pepperberg, 2004, Schuck-Paim et al., 2009, Werdenich and Huber, 2006); if not after minimal experience (Funk, 2002). Overall findings from the string-pulling paradigm suggest that parrots and corvids can discriminate between strings that are baited with rewards and those without rewards (Bagotskaya et al., 2012, Funk, 2002, Heinrich, 1995b, Heinrich and Bugnyar, 2005, Krasheninnikova et al., 2013, Pepperberg, 2004, Schuck-Paim et al., 2009, Werdenich and Huber, 2006), with some species capable of determining connectedness through physical continuity (Bagotskaya et al., 2012, Heinrich, 1995a, Krasheninnikova et al., 2013). Mixed performances have however been reported when subjects are presented with more difficult tasks, such as crossed rewarded and non-rewarded strings. Kea (*Nestor notabilis*), spectacled parotlets (*Forpus conspicillatus*) and ravens (*Corvus corax*) have demonstrated abilities to discriminate between rewarded and non-rewarded crossed strings of the same colour, whereas rainbow lorikeets (*Trichoglossus haematodus*), green-winged macaws (*Ara chloroptera*) and sulphur-crested cockatoos (*Cacatua galerita*) fail to solve this task (Heinrich, 1995a, Krasheninnikova et al., 2013, Werdenich and Huber, 2006). Subjects' performances may however improve when different colours are used to help visually track the course of the rewarded crossed string (Krasheninnikova et al., 2013). However, hyacinth macaws (*Anodorhynchus hyacinthinus*), Lear's macaws (*Anodorhynchus leari*), blue-fronted Amazons (*Amazona aestiva*), and crows (*C. cornix*) failed to solve crossed strings tasks even when the strings were different colours, suggesting that this problem may be particularly challenging (Bagotskaya et al., 2012, Schuck-Paim et al., 2009).

While numerous species of birds have been tested on vertical string-pulling tasks, only parrots and corvids appear capable of solving complicated discriminations between strings. Another common approach to assess physical cognition in non-tool using and tool-using species, particularly primates, is through horizontal means-end physical support problems.

Horizontal Support Problems

Like string pulling, the retrieval of rewards on horizontal support problems requires an ability to discriminate between cues pertaining to physical relationships (spatial relationships, contact, surface continuity), and hence may also suggest an understanding of “Folk Physics” (Povinelli, 2000). There are two main types of means-end support problem: the On problem, where subjects are required to discriminate between retrieving rewards that are placed either on, or off supports; and the Connected problem, requiring the discrimination between pulling a functional (i.e. a continuous connection to the reward), rather than a non-functional support (i.e. a disrupted connection separated by a gap).

Although great apes essentially demonstrate spontaneous comprehension of the connected problem (Herrmann et al., 2008, Mulcahy et al., 2012), there are few reports of such abilities in birds. Funk (2002) however, showed that young kakariki (parakeets) could retrieve out-of-reach seeds by pulling a piece of paper that the seeds were resting on into their cage. One blue-fronted Amazon (parrot) learned, although after a considerable number of trials, to retrieve food that was resting on, rather than off, cloths of varying configurations (de Mendonca-Furtado and Ottoni, 2008). Pigeons also required an extensive number of trials to solve similar tasks (Schmidt and Cook, 2006). The only convincing evidence that any species of bird possess an advanced ape-like comprehension of the connected problem is demonstrated by the kea; which rapidly solved both the On and Connected problems (Auersperg et al., 2009). In this study, one of six birds (Anu, a juvenile) demonstrated spontaneous comprehension of the Connected

problem, by pulling continuous, rather than disrupted, wooden slats to successfully retrieve food rewards. Impressively, this individual correctly chose the connected slat in 10 out of his first 10 trials on the problem (Auersperg et al., 2009). However, to date, there is only one published study detailing the performances of a single species of parrot, the kea, on the means-end Connected problem (Auersperg et al., 2009) and comparable studies remain to be reported for corvids. Ravens and crows, however, show an ability to solve potentially more complicated crossed support problems, although, in contrast to apes, the corvids did not appear to comprehend the causal principles of this task (Albiach-Serrano et al., 2012).

Together, these findings suggest that parrots have some understanding of the physical properties of tools, even if they are not regularly presented with such challenges in the wild. Experimental paradigms that make tool-use necessary for the acquisition of food in captivity may therefore provide an essential opportunity to reveal what non-tool-using species understand about the physical relationships of objects. However, while some species show apparent capacities for spontaneous problem solving on simple means-end problems, comparisons between species on more complicated tasks, that initially require trial-and-error experience, may be influenced by differences in subjects' previous experience of particular materials, their training regimes, or exposure to similar types of problems.

Trap-Tables, Trap-Tubes and Transfer Tasks

Another method used to assess whether previous experience influences performances on subsequent tasks is to present subjects with novel, but functionally equivalent transfer tasks. Subjects can first learn to solve an initial problem through trial and error. After mastering this problem, subjects are then presented with a novel transfer task. As the presentation order of the initial task and the transfer task can be counterbalanced across subjects, subjects that slowly learn to solve the initial task, but spontaneously solve the transfer task may reveal capacities for generalised learning. Such abilities

suggest that subjects may comprehend similarities in the underlying causal relationships of the problems.

Two tasks that share similar functional problems are the Trap-Tube (Seed et al., 2006) and Trap-Table problems (Povinelli, 2000). Both tasks require subjects to avoid a functional trapping hole by attending to surface continuity; somewhat similar to the means-end Connected problem. However, success on the Trap-tube and Trap-Table problems have provided mixed results. While rooks (Seed et al., 2006), New Caledonian crows (Taylor et al., 2009) and apes (Seed et al., 2009b) demonstrate a causal understanding of the Trap-Tube problem, six kea, three red-and-green macaws, and a sulphur-crested cockatoo failed to avoid the traps (Liedtke et al., 2010). Apes have also failed to transfer learned information between these two problems (Martin-Ordas et al., 2008), whereas New Caledonian crows that were capable of solving a Trap-Tube problem could also solve a Trap-Table problem (Taylor et al., 2009). Such findings provide tentative evidence that certain animals are capable of solving problems based on a causal understanding object relationships. However, further evidence of such abilities is required to bolster support for such findings and new paradigms that can be applied across a variety of tool-using and non tool-using species are necessary.

In the current study I assess the comprehension of object relationships in two species of captive hand-reared Neotropical parrots, using two different means-end tasks; the Connected problem, and a new paradigm, the Trap-Gaps problem. Both means-end tasks were developed to incorporate novel, but functionally analogous transfer problems. Performances on such transfer problems may therefore reveal whether parrots are capable of generalising learned information across novel tasks by attending to causally relevant information.

Subjects were initially presented with the Connected problem, which required an ability to discriminate between pulling connected or disrupted lengths of

strings or cloths to retrieve an otherwise out-of-reach reward. Subjects were first presented with problems using familiar materials, and then presented with a novel transfer task using unfamiliar, but functionally equivalent, materials. The purpose of familiarising subjects with the initial testing materials was first to eliminate any neophobic responses subjects may have towards the novel objects, which might impair their performances, and second, to provide subjects with limited experience of the functional properties of the materials. Hence, if familiarity with materials improves subjects' performances, we may predict subjects to solve the initial test phase with fewer errors than the novel transfer phase. Alternatively, subjects that solve the novel transfer phase with fewer errors than the test phase may instead show capacities to transfer relevant information across problems irrespective of their prior experience with certain materials. This procedure therefore addresses whether subjects require some familiarity of materials to understand functional properties, or whether subjects are able to infer material functionality from visual information alone.

In a second experiment, using a newly-designed task, the Trap-Gaps problem, subjects were assessed on their ability to discriminate between pulling food-trays through gaps while attending to the respective width of the gaps and size of the trays. Subjects were presented with two novel tasks; one in which the size of the gaps varied, but the size of the trays remained constant and another task where the size of the trays varied, but the size of the gaps were held constant. Hence, subjects may learn the object relationships through trial-and-error in the first task, but could potentially solve the second task spontaneously if they transferred learned principles of object relationships across problems.

5.0.3: General Methods

Subjects

Subjects were approximately nine months old when tested on the Connected Problem and 33 months old when tested on the Trap-Gaps problem. Subjects had no previous experience with means-end problem solving tasks but had experience on foraging problems requiring object manipulation, such as up-turning plastic cups to retrieve concealed food rewards.

5.1: The Connected Problem

5.1.1: Methods

Apparatus

Subjects were presented with a typical black A4 letter-tray (35cm x 25cm) attached horizontally to the exterior of their enclosure at 1.5m in height (Figure 5.1). The tray was partitioned in the middle by an opaque barrier (4cm x 30cm). Depending on the test condition, either a length of green string or white cloth was placed on either side of the partition. A small plastic lid containing a preferred food item was attached at the distal end of each string/cloth.

Procedure

Subjects were transferred to a visually isolated but familiar experimental enclosure (2m³) and tested individually. The presentation order of trials commencing with either strings or cloths was counterbalanced across subjects. Strings were coloured green with a white 2cm diameter plastic lid attached at the distal end. Cloths were white in colour, with a blue 2cm

diameter lid attached at the distal end (Figure 5.1). Both lids were baited with a preferred food reward (crumbled Lafeber Nutri-Berries). Trials were completed when subjects pulled one of the strings/cloths. Subjects were presented with one block of ten trials per day and were only allowed one choice per trial. Subjects were not rewarded for pulling disrupted strings/cloths. If subjects pulled the disrupted string/cloth, the experimenter immediately retrieved the string/cloth from the subject. The experimenter prepared the strings/cloths so that they were initially out of the subject's reach; simultaneously positioning the strings/cloths on either side of the partition. When the strings/cloths were in position, the experimenter waited five seconds before simultaneously moving the strings/cloths forward so that they were within reach of the subject. Subjects were presented with a total of 10 blocks of 10 trials each, independent of their performance or test condition (i.e. subjects participated in exactly 100 trials each). Subjects were not corrected for side biases. All trials were recorded on a digital video camera (JVC Everio, Model No. GZ-MG645BEK, Malaysia). During trials, the experimenter placed his hands behind his back and monitored the subject's behaviour via the video display.

Training Phase: food/no food discrimination

During training, subjects were presented with two 5cm long (continuous) strings/cloths (cloth 2.5cm wide), depending on their assigned condition. Only one string/cloth was baited with a reward. Hence, subjects not only had to habituate to pulling a novel material, but also differentiate between selecting baited rather than un-baited strings/cloths. To proceed to test, subjects were required to retrieve the reward five consecutive times in one block of 10 trials. A relaxed criterion (i.e. not significant according to a binomial test) was used during training to ensure that subjects had minimal experience pulling strings/cloths, while ensuring that subjects were both motivated and physically capable of retrieving the reward. The position of the baited and un-baited strings/cloths was pseudorandomised across trials and never occurred on the same side for more than three consecutive trials. Once subjects

reached the training criterion, they proceeded to the test condition in the following session.

Test Phase: Connected problem

Subjects in the test condition were presented with an identical, but elongated, version of the strings/cloths (16cm) as during the training sessions. Rewards were placed in both lids attached to the distal ends of the strings/cloths. Only one string/cloth was continuous, while the other was separated in the middle by a 1.5cm gap (Figure 5.1). To retrieve the reward, subjects had to choose the continuous string/cloth. The positioning of the continuous and discontinuous strings/cloths was pseudorandomised as in the Training phase. Trials were prepared within the subject's view, with both the continuous and discontinuous strings/cloths positioned simultaneously on the tray.

Novel Transfer Phase

Subjects were considered to have demonstrated an understanding of the Test condition once they reached a criterion of 15 or more correct responses over two consecutive blocks of ten trials (a result that is significant according to a Binomial test with a probability of choosing either side set at 0.5). Once subjects reached this criterion, they were presented with a novel transfer task on the following day. The transfer task was functionally equivalent to the initial task i.e. transferring from pulling cloths to pulling strings and vice versa, however subjects had no prior experience with the novel transfer materials. So, subjects that had received training to pull strings were then tested on pulling strings, and then transferred to pulling cloths and vice versa. Subjects were deemed to have transferred relevant, learned rules across tasks if they rapidly solved the problem by making at least 15/20 correct trials in their first two consecutive blocks.

Statistical Analysis

I used a binomial test (with a probability of choosing either side set at 0.5) to determine our transfer criterion of at least 15/20 correct trials over two consecutive blocks of 10 trials (significant at 0.05). A non-parametric Mann-Whitney test was used to compare between-species differences in the number of errors to reach the transfer criterion. All tests were two-tailed, with alpha set at 0.05. Exact tests were reported for all analyses, following the procedures outlined by Mundry and Fischer (1998).

5.1.2: Results

Both species rapidly learnt to pull the strings/cloths. Subjects typically grasped the accessible end of the materials with their beak, as this procedure possibly required careful dexterity. Subjects then proceeded to retrieve the materials using either their beak or feet.

Training Phase

Macaws made between 0-30 errors before proceeding to the test condition (Figure 5.2). Three of four birds (No.4, No.5 and No.8) made correct choices on their first trial of the training condition

Caiques performed similarly to macaws, making between 0-13 errors before proceeding to the test condition (Figure 5.2). Three of four caiques (Green, Purple and Red) also chose the baited side on their first trial of the training condition.

Test Phase

All subjects from both species participated in the Connected Problem (Figure 5.3). All macaws chose the correct side on their first test trial. Two macaws, No.2 and No.8, rapidly reached criterion in the test condition after making a total of eight and five errors, respectively (Figure 5.4). While No.2 made four errors on the first block and another four errors on the second block, this bird successfully solved all 10 trials on its third block before proceeding to the transfer phase. The other successful macaw, No.8, made two errors on its first block and three errors on its second block before proceeding to the transfer phase.

The remaining two macaws, No.4 and No.5, failed to reach criterion for the transfer task within 100 trials. However, No.4 made eight correct choices in her first 10-trial block, and No.5 made nine consecutive correct choices in his third block. Although No.5's performance on the third block did not reach the predetermined criterion of success for transferring to the second task, this bird's performance remains significant according to a binomial test, with a probability of choosing either side set at 0.5 (9/10 correct; $p < 0.05$).

Two of four caiques chose the correct side on their first trial. Two caiques, Gold and Green, reached transfer criterion after making five and 17 errors respectively (Figure 5.4). Gold spontaneously reached binomial significance after making eight consecutive correct choices and only one error in his first 10-trial block (i.e. 9/10 correct; $p < 0.05$). Gold then made four errors on his second block before proceeding to the transfer phase. Figure 5.4 illustrates that Green made 19 errors before reaching criterion in the test phase. However, Green only completed 8 out of 10 trials before his first block was terminated (after 60min of inactivity). Hence, Green made 5 errors out of 8 trials during his first block, rather than 7 errors as depicted in Figure 5.4. Statistical analyses, as reported above, were therefore made using the 17 errors that Green made before reaching criterion (i.e. Block 1 = 5 errors; Block 2 = 7 errors; Block 3 = 2 errors; Block 4 = 3 errors).

The remaining two caiques failed to reach the criterion for transfer within 100 trials. Of those caiques that failed to reach criterion, Purple made eight correct choices in his second block, with six consecutive correct choices (significant according to a binomial test (with a probability of choosing either side set at 0.5), and Red's poor performance was due to a side bias, which began from his first trial and persisted throughout testing.

There were no between-species differences in the number of errors to reach the initial criterion for transfer; Mann-Whitney Test, $U = 1.5$, $N_1 = 2$, $N_2 = 2$, $p = 1.00$. None of the subjects that reached the transfer criterion solved the transfer task within their first two blocks, or with fewer errors than in their previous task.

Transfer Phase

Two macaws (No.2 & No.8) and two caiques (Gold & Green) participated in the transfer task (Figure 5.4). Only one subject, No.8, successfully reached criterion on this task, making a total of 26 errors across six blocks. This subject was then presented with a further two blocks on the initial problem, making five and four errors respectively. All of the other subjects that participated in the transfer task (No.2, Gold and Green) failed to reach criterion.

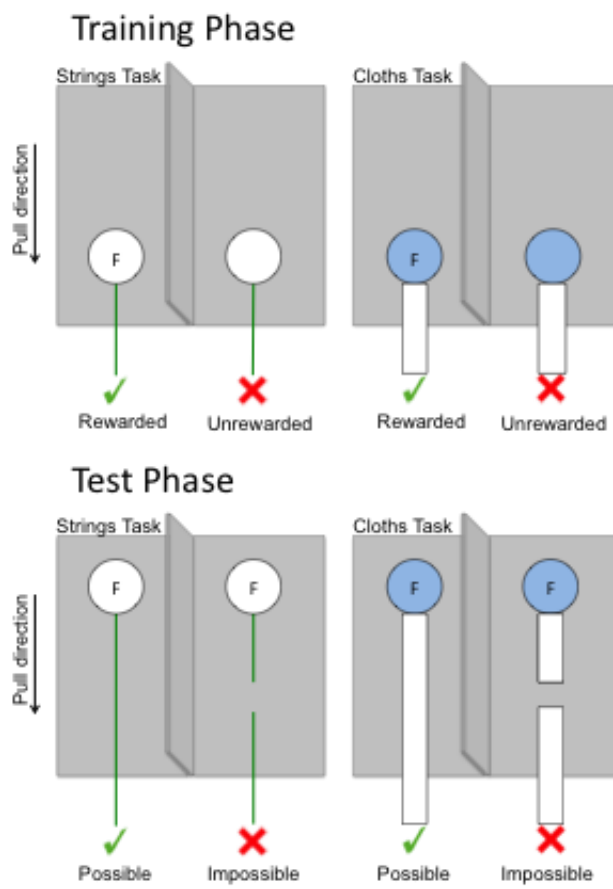


Figure 5.1. Schematic of the Training and Test apparatus for the Connected problem (not to scale).

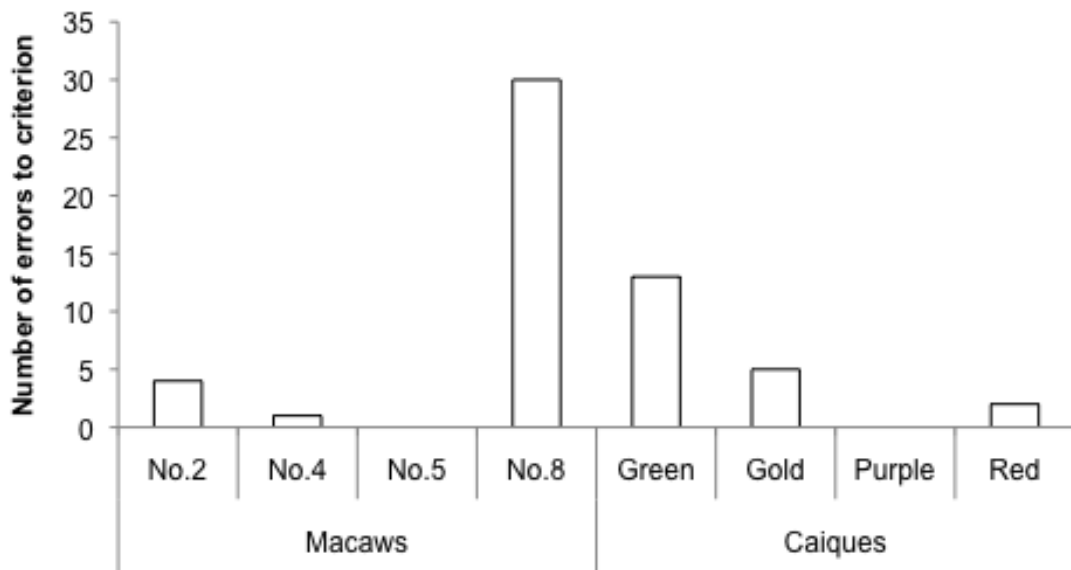


Figure 5.2. Number of errors to reach a criterion of 5 consecutive correct choices during training trials.

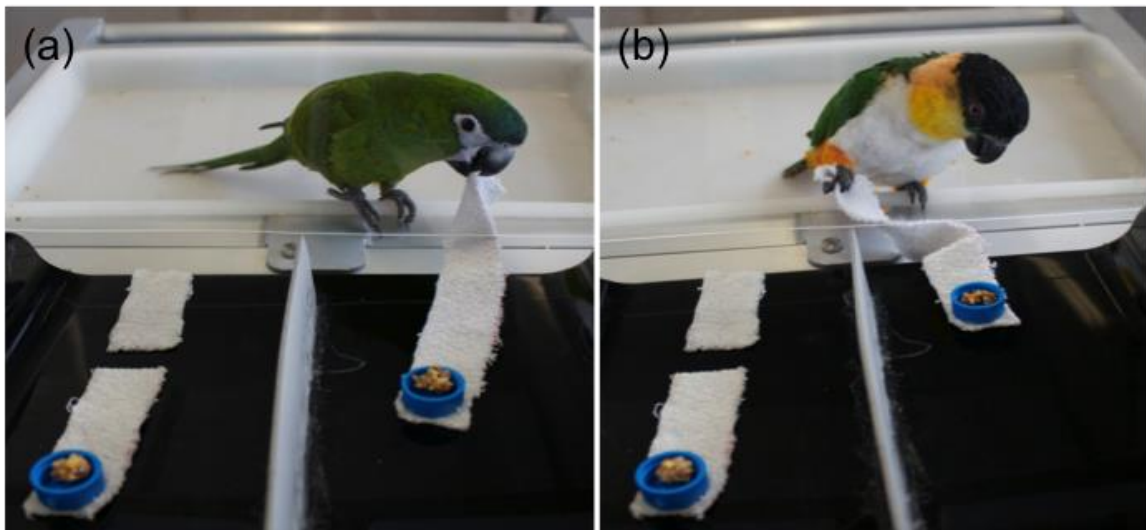


Figure 5.3. (a) A red-shouldered macaw and (b) A black-headed caique pulling cloths on the Connected problem.

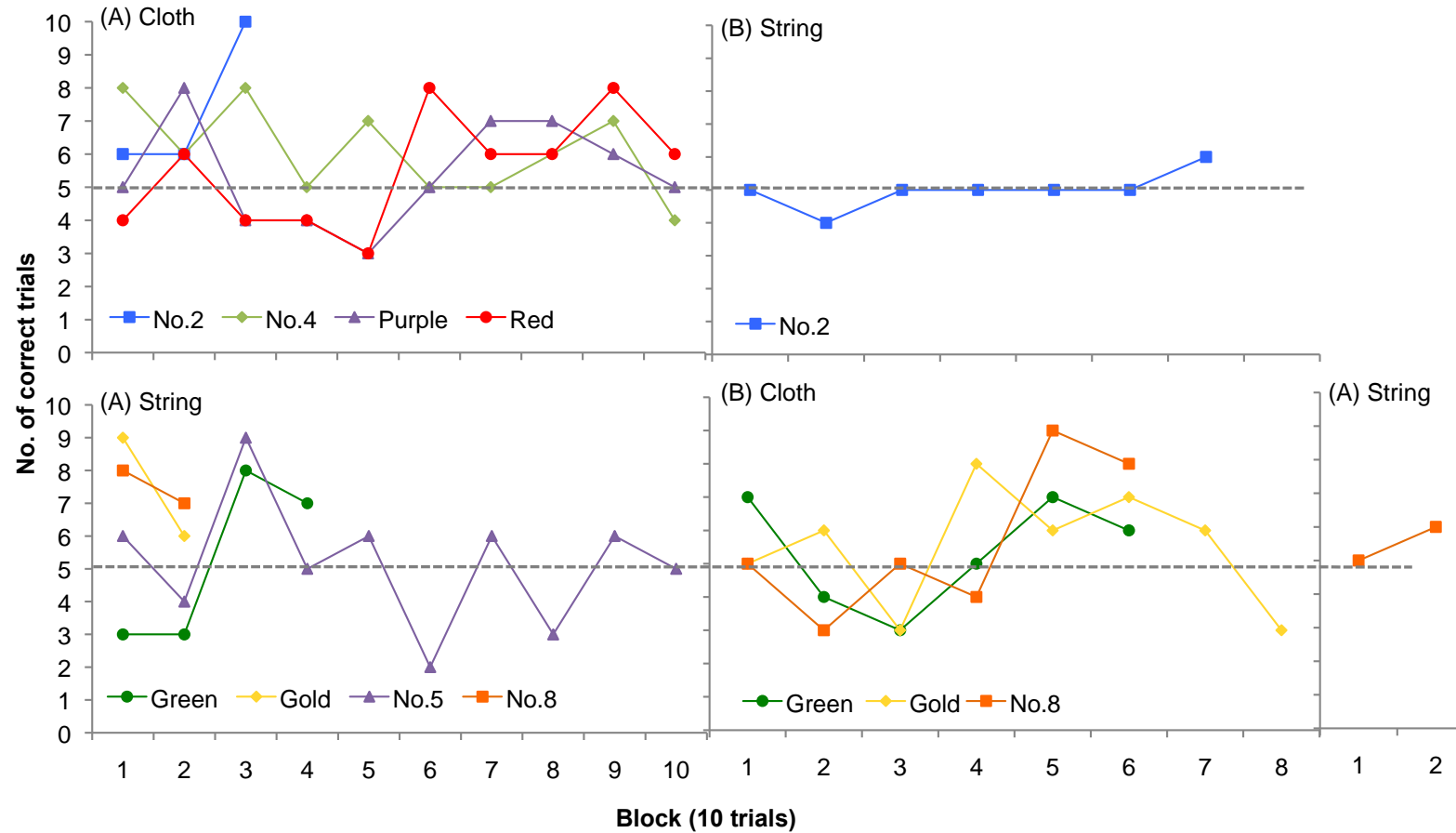


Figure 5.4. Performances on the means-end connected problems using (A) familiar materials and (B) novel materials. The horizontal dotted line in each graph shows chance performance (5 out of 10 trials correct). Subjects received a total of 10 x 10-trial sessions. Green only completed 8, rather than 10, trials in his first block.

5.1.3: Discussion

Red-shouldered macaws and black-headed caiques could spontaneously discriminate between pulling baited, rather than un-baited, strings/cloths to retrieve an otherwise out-of-reach food reward. After minimal experience on this training task, subjects were then required to discriminate between pulling either connected or disrupted strings/cloths to retrieve rewards. Two macaws and two caiques rapidly reached the transfer criterion, demonstrating near spontaneous comprehension of the connected problem.

Subjects, however, showed inconsistent performances across blocks, resulting in a relatively low transfer success considering the overall within-session performances of some individuals. Consequently, our criterion, which required consistent performances across two successive blocks, may understate our subjects' comprehension of the task. One caique, Gold, for example correctly chose the continuous string on his first 8 trials; reaching 9 out of 10 correct choices in his first block. Gold's performance here is significantly above chance ($p < 0.05$; according to a binomial test), suggesting that he had a spontaneous comprehension of the connected problem. However, Gold failed to perform above chance on his second block. Likewise, one macaw, No.5, also made one error on the first trial of his third block, after which he chose the correct string for the following nine trials. Although No.5's performance here was significantly above chance, this bird failed to reach the predetermined transfer criterion within 100 trials.

The variable performances of subjects across blocks may suggest that macaws and caiques were not able to retain previously learned information to aid their performances across subsequent blocks. This explanation, however, fails to account for the spontaneous success of subjects during their initial training and testing trials. Subjects' performances appeared to plateau across blocks, possibly a result of their increasing familiarity of the rewarded materials. Subjects' inconsistent performances may therefore be associated

with the onset of certain motivational issues. Hence, as subjects became increasingly familiar with the task they may have become less motivated to interact with the rewarded materials, and more interested in exploring the relatively less familiar, but unrewarded, materials.

Of the four individuals that rapidly reached criterion for transfer, all performed poorly when they were presented with unfamiliar materials. Subjects therefore appeared to have failed to generalise relevant information, based on physical relationships, to solve the novel transfer task. Red-shouldered macaws and black-headed caiques, however, show diverse exploratory behaviours when repeatedly presented with a variety of objects (Chapter 3.2), yet their interactions with novel objects are initially constrained by neophobic behaviours (Chapter 3.1). The presentation of unfamiliar materials may have therefore induced neophobic responses, requiring subjects to first explore the objects before establishing goal-directed behaviours. Consequently, minimal familiarity and experience with materials, as provided during the initial training phase, may be required to reduce neophobic responses, and hence promote goal directed behaviours. Hence, highly familiar or novel materials may influence subjects' performances by diverting their attention from the goal-directed retrieval of food rewards, towards greater object exploration and manipulation. Subsequent studies may therefore benefit by first habituating subjects to all materials in an attempt to control for differences in neophobic or neophilic responses across training, testing and transfer conditions.

Although subjects spontaneously retrieved baited rather than un-baited materials during the training trials, they may during this process have also inadvertently formed an association between the reward and the continuous material. Hence, as subjects were presented with the same (albeit shortened) materials on the Connected problem as in the Training problem, they could potentially ignore the novel configuration of a disconnected string/cloth and solve the problem through previously learned contextual associations; without any concept of connectedness. Hence, subsequent studies may also benefit from using training materials that differ from those used in the testing

conditions. In this study however, subjects experienced the testing materials during training but had no experience with the materials in the transfer condition. As a result, prior experience of materials appeared to facilitate success on subsequent tasks requiring physical manipulation, while novel materials impeded subjects' performances.

While the parrots in this study failed to rapidly solve the transfer task when they were presented with novel materials, highly neophobic ravens spontaneously solved a simple, vertical string-pulling problem using novel materials. Heinrich (1995a), conditioned ravens to retrieve a food reward by pulling up a light-coloured twine string. After the ravens became familiar with this task they were subsequently presented with a choice between pulling the familiar, but this time un-baited, light-coloured twine string, or a novel but baited, dark green woven shoelace. The ravens spontaneously selected the novel baited shoelace, suggesting that they were attending to the presence of a reward, rather than particular materials. Apes also show an ability to understand the Connected problem when presented with familiar and unfamiliar materials (Herrmann et al., 2008). However, apes required additional experience to solve a more complex connectivity problem, when presented with unfamiliar plastic canes, rather than familiar cloth (Herrmann et al., 2008). Moreover, apes perform better on the Connected problem when they were presented with naturally familiar tools, such as sticks fashioned from tree branches which they are likely to have had extensive experience manipulating, rather than artificial familiar tools made from plastic with which they may have had less experience (Mulcahy et al., 2012).

Cotton-top tamarins (*Saguinus oedipus*), which do not naturally use tools, appear to successfully transfer functionally relevant information to solve novel means-end problems that vary in irrelevant features, such as colour or shape (Hauser et al., 1999). However, tamarins with experience as tool users were more successful than tool-inexperienced tamarins when selecting tools based on their functionally relevant features (Hauser et al., 2002b). Furthermore, tool-naïve tamarins and closely related common marmosets (*Callithrix*

jacchus) that had no prior training or experience on means-end tasks showed no preferences for functional characteristics of tools (Spaulding and Hauser, 2005). Apes also appeared to have difficulty transferring learned information across functionally identical problems involving trapping holes (Martin-Ordas et al., 2008, but see Martin-Ordas et al., 2012). Together, these findings suggest that familiarity with materials may be necessary for animals to develop an understanding of the physical properties of objects that they interact with. Moreover, such experience also appears to be particularly valuable when animals are presented with increasingly challenging problems.

The performances of macaws and caiques on the Connected Problem, may however be considered particularly noteworthy for two reasons. First, subjects were only 9 months old when tested, which is relatively young when compared to findings from apes, which ranged between 3-31 years old, with a median age of 11 (Herrmann et al., 2008). Stereotyped object manipulations have been observed to precede more sophisticated tool-related behaviours in juvenile New Caledonian crows (Kenward et al. 2006). Hence, age and life experience may play an important role in advancing physical cognition. Moreover, proficient tool-use in primates—which may regularly use tools—can take years of practice to achieve (Fragaszy et al., 2010, Matsuzawa, 1994). Second, the performances of macaws and caiques on this task have rarely been revealed in other animals without extensive training with materials.

The performances of red-shouldered macaws and black-headed caiques on the connected problem has only been rivalled by one other avian species; the kea, an alpine parrot indigenous to New Zealand (Auersperg et al., 2009). In this study, subjects were provided with minimal experience of the functional properties of materials before being presented with the connected problem. One of six birds (Anu, a juvenile) chose the connected side in 10 out of his first 10 trials, demonstrating spontaneous comprehension of the task. However, we might expect similar performances from other species of parrots and corvids, considering their motivation to pull vertical strings to retrieve food

rewards (Heinrich and Bugnyar, 2005, Krasheninnikova and Wanker, 2010, Pepperberg, 2004), discriminate between certain physical properties of vertical strings (Heinrich, 1995a, Krasheninnikova et al., 2013, Pfuhl, 2012, Schuck-Paim et al., 2009), and horizontal support problems (Albiach-Serrano et al., 2012,).

In contrast to our subjects', four pigeons, were initially presented with 140-200 food/no-food discrimination training trials. Yet after such experience, all pigeons failed to perform above chance within their first 20 trials of the connected problem (Schmidt and Cook, 2006). Similarly, one Asian elephant, Authai a 6 year-old female, first participated in 100 food/no-food discrimination trials (of which she could retrieve both trays, and hence a reward, in her first 50 trials), and 250 on/off discrimination trials, before being presented with the connected problem. This elephant then proceeded to choose the connected side in eight out of her first 10 trials, but only reached binomial significance after 40 trials (Irie-Sugimoto et al., 2008).

This study reveals that macaws and caiques can spontaneously solve a means-end problem that requires an ability to discriminate between the presence and absence of a food reward. Moreover, both species rapidly solved a more complicated connected problem when using familiar materials. Yet subjects' performances on the connected task were impaired when they were presented with novel materials, suggesting that familiarity and experience may be necessary for these species to learn the functional properties of materials. However, as subjects in this study were tested on familiar materials that were identical to the materials used during the training sessions, it remains unclear whether subjects successfully discriminated between connected or disrupted materials or whether they simply failed to attend to the disrupted materials. A new Trap-Gaps transfer paradigm using a novel test and transfer condition was therefore designed to further investigate physical comprehension of means-end object relationships in parrots.

5.2: The Trap-Gaps Problem

5.2.1: Methods

Apparatus

Task (A): Small and large gaps/medium sized cups

Two identical yellow cups (60mm diameter x 20mm deep) were baited with food rewards and positioned out of the subjects reach at the distal end of a partitioned A4 letter tray (as above). A 200mm long green string was attached to each cup and placed within reach of the subject, allowing the cups to be pulled towards the cage (Figure 5.5).

To retrieve the food reward, subjects were required to discriminate between two different sized gaps: one gap was large enough to allow the passage of the cup (70mm wide x 50mm high), whereas the other gap restricted access to the cup (50mm wide x 50mm high). Both gaps were positioned towards the front of the apparatus, approximately 170mm from the subject. To access the reward, subjects were required to select, and then pull, the string attached to the appropriate cup by attending to the size of the intervening gap.

Task (B): Small and large cups/small gaps

In this experiment, both gaps were positioned in the same location as above, but each gap was the same size (65mm x 50mm high). Subjects were presented with two baited blue cups containing equal rewards, one large (75mm diameter, 20mm deep) and one small (55mm diameter x 20mm deep). Apart from their size, both cups were identical. The gaps were large enough to allow passage of the small cup, but restricted access to the large cup. To access the reward, subjects were required to attend to the size of the cups, with respect to the gap size (Figure 5.5).

Procedure

The apparatus and strings were set in position at the beginning of each trial, with the location of the accessible reward pseudorandomised so that it did not occur on the same side over more than two consecutive trials. The apparatus was positioned so that the strings were initially out of the subjects reach. The experimenter then waited until the subject was positioned within 10cm of the front of the apparatus. A five second delay was then administered before the experimenter simultaneously moved both strings forward so that they were within the subjects reach.

Subjects were only allowed to pull one string per trial. Subjects were considered to have made a correct choice if they retrieved the reward. Subjects that pulled the incorrect string were not rewarded. Subjects were provided with a maximum of 10 trials per day. The apparatus was re-baited out of view of the subject. The outcome of each trial was coded live, and recorded on a digital camcorder (JVC Everio, Model No. GZ-MG645BEK, Malaysia).

Training Phase

During training sessions, subjects were presented with two green cups (55mm x 20mm deep), each attached to a 200mm long piece of green string. Subjects were not presented with gaps during training trials and both cups could be retrieved by pulling their respective strings. However, during training only one cup was baited. To proceed to the test condition, subjects were required to reach a successful criterion of seven consecutive correct choices in one block of 10 trials. This procedure ensured that the subjects were attending to the cups and could competently pull the string to retrieve the reward. Once subjects reached the training criterion, they proceeded to the test condition on the following day.

Subjects were considered to have developed a side bias if they chose the same side over six or more trials. To correct for side biases, the non-preferred side was consistently baited until the subject retrieved the reward over two consecutive trials. The presentation order then resumed to its original pseudorandomised configuration.

Testing Phase

The presentation order of Task (A) and Task (B) was counterbalanced across subjects. Subjects were required to reach a successful criterion of 7 consecutive correct choices in one block of 10 trials, or 9 out of 10 correct in one block of 10 trials (a result that is significant according to a Binomial test (with a probability of choosing either side set at 0.5) before transferring between experiments.

Subjects that chose the same side over six or more consecutive trials were considered to have developed a side bias. To correct for side biases, subjects were provided with the training discrimination task, with the baited cup presented on the non-preferred side. Subjects were presented with one 10-trial session per day using this configuration until they selected the baited cup (on the non-preferred side) for two consecutive trials. Subjects then reverted back to the pseudorandomised testing condition. Corrective trials from the training task were not included in the analysis. Testing ceased if a subject failed to reach the initial test criterion within 200 trials (20 blocks). Subjects that failed to reach criterion in the first task were not presented with a transfer task. Testing also ceased for the transfer task if subjects failed to reach criterion with fewer errors than their previous task.

To determine whether subjects retained information from their past experience with the apparatus, subjects that reached criterion both on their initial task and on the transfer task were re-tested with one additional block of 10 trials on their initial task (Table 5.1: Task 1b).

Statistical Analysis

Independent t-tests were used to compare the number of errors for each species to reach training criterion. Subjects were considered to have solved the tasks if they successfully retrieved the food in either seven consecutive correct choices in one block of 10 trials, or nine correct choices in one block of 10 trials. A binomial test was used to assess the statistical significance of these performance criteria. Alpha was set at 0.05.

5.2.2: Results

Training Phase

Both species rapidly solved the training discrimination task. There were no significant between-species differences in the number of errors to reach the initial training criterion (Figure 5.6); independent t-test, $t = 0.736$, $df = 6$, $p = 0.489$ (macaws mean = 10.00 ± 3.00 SEM, caiques mean = 7.00 ± 3.00 SEM).

As there were no between-species differences in errors to reach criterion during the training sessions, two individuals from each species were randomly assigned to either receive trials commencing with changes to the size of the cups (where the gap size remained consistent), or changes to the size of the gaps (where the cup size remained consistent). Hence, four individuals (two caiques & two macaws) participated in each of the two conditions. There were also no significant differences in errors to reach the training criterion between the two groups that either began the test trials with cups or gaps; independent t-test, $t = 1.287$, $df = 6$, $p = 0.246$ (cups first mean = 11.00 ± 3.00 SEM, gaps first mean = 6.00 ± 3.00 SEM).

Test and Transfer Phase

Cups Problem

All four subjects that commenced trials with the cups problem reached the criterion to transfer to the second task (mean number of errors: 41.00 ± 11.98 SEM; mean number of trials: 90.50 ± 24.85 SEM; Table 5.1).

Only two individuals in this group (No.4 and Red), however, reached criterion in the transfer condition. Of the two birds that reached criterion, one macaw, No.4, showed similar performances on both tasks; making 20 errors out of 45 trials on the first task, and 21 errors out of 68 trials on the second task. Hence, No.4 showed no transfer of learned information across tasks. However, when re-tested on the first problem, this bird successfully chose the correct cup on all 10 trials ($p < 0.05$ according to a binomial test). One caique, Red, spontaneously solved the transfer task. Red made 57 errors out of 133 trials on the first task, but reached the second criterion without making any errors (errors: 0; trials 7; binomial test; $p < 0.05$). Although trial-by-trial data for this bird is not presented in Table 1, this subject chose the correct side for its first nine consecutive trials of the transfer task, only choosing the unrewarded side only on its 10th trial. Red was then retested on the first problem and successfully chose the correct cup on all 10 trials ($p < 0.05$ according to a binomial test with a probability of choosing either side set at 0.5).

Gaps Problem

Only two individuals that commenced trials with the gaps problem successfully reached criterion (No.5 and Gold). Of these successful birds, No.5 made 24 errors out of 67 trials, and Gold made 10 errors out of 32 trials (mean number of errors: 17.00 ± 7.00 SEM; mean number of trials: 49.50 ± 17.50 SEM; Table 5.1). Two subjects (No.8 and Purple) did not reach the

initial task criterion within 200 trials, and therefore were not presented with the transfer task.

Of the two subjects that participated in the transfer task, one subject, No.5, reached criterion in the transfer task with fewer errors than the initial task (Test task: 24 errors in 67 trials; Transfer task: 11 errors in 38 trials; Table 5.1). While the other successful subject, Gold, rapidly reached criterion in the transfer task, it made twice as many errors than on its first task (Test task: 10 errors in 32 trials; Transfer task: 20 errors out of 46 trials). After reaching criterion on the cups transfer problem, two subjects (No.5 and Gold) were retested with a further 10 trials on the initial gaps problem (Table:5.1; Task 1b). Gold made three errors and No.5 made five errors on their first 10 trials of this task. Both subjects therefore failed to reach criterion when retested on their initial task (binomial test with a probability of choosing either side set at 0.5; $p > 0.05$).

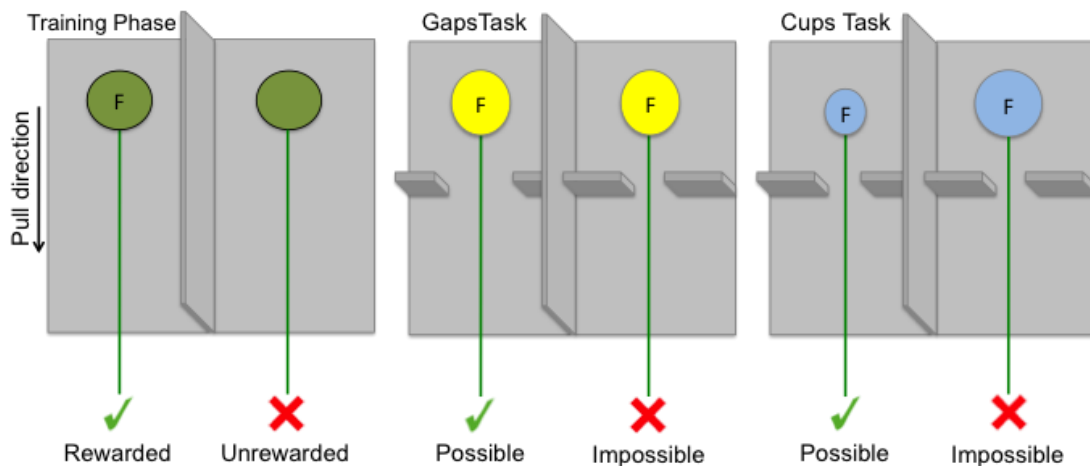


Figure 5.5. Schematic of the Trap Gaps Training and Test apparatus (not to scale). “F” indicates a food-reward tray, which can be pulled toward the subject via a green string. The Gaps Task can only be solved by attending to the large gap, whereas the Cups Task can only be solved by attending to the small tray.

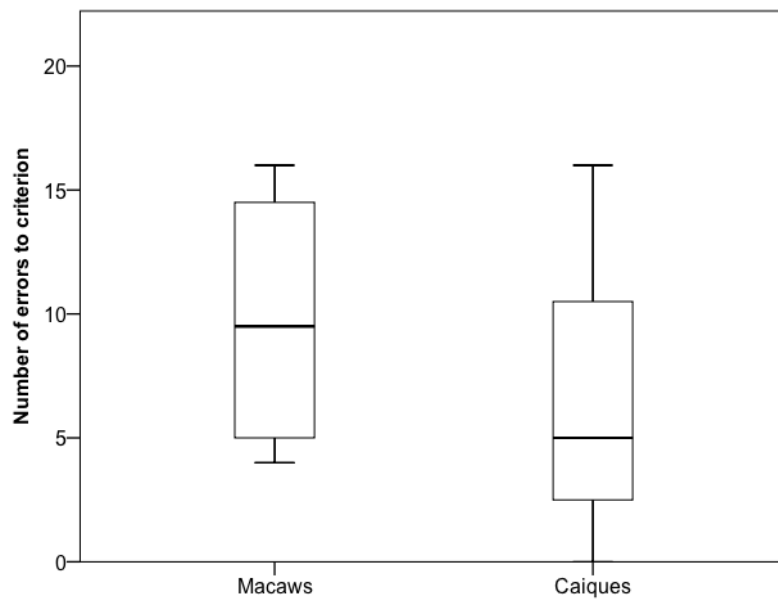


Figure 5.6. Box and Whisker plot of Inter Quartile Range (25%-75%) and median number of errors for each species to reach criterion in the training session.

Table 5.1. Number of errors to reach a binomially significant criterion for groups commencing with the cups task and then transferring to the gaps task and vice versa. Total number of trials are presented in parentheses. Task 1b shows errors for the first 10 trials. Boxes denoted by a “+” indicates that individuals failed to reach criterion within the corresponding number of errors; “n/a” indicates that subjects were not presented with the transfer test as they did not reach criterion for the previous task; “*” indicates that subjects reached binomial significance within 10 trials on ($p < 0.05$).

<u>SUBJECTS</u>	<u>TASK 1: Cups</u>	<u>TASK 2: Gaps</u>	<u>TASK 1b: Cups</u>
No.2	21 (50)	+ 33 (100)	n/a
No.4	20 (45)	21 (68)	0* (10)
Green	66 (134)	+ 70 (139)	n/a
Red	57 (133)	0* (9) / 1* (10)	0* (10)
	<u>TASK 1: Gaps</u>	<u>TASK 2: Cups</u>	<u>TASK 1b: Gaps</u>
No.5	24 (67)	11 (38)	5 (10)
No.8	+ 91 (202)	n/a	n/a
Gold	10 (32)	20 (46)	3 (10)
Purple	+ 98 (216)	n/a	n/a

5.2.3: Discussion

While six of eight parrots (three macaws and three caiques) learned to solve their initial Trap-Gaps problem, subjects' performances to achieve a successful criterion varied considerably. Such variable performances suggest that the ability to discriminate between the size relationships of the cups and gaps was a particularly difficult task for subjects to learn. Four of six birds (two macaws and two caiques), however, solved the transfer task; one caique spontaneously reached criterion without making any errors, and one macaw solved the problem with less than half as many errors than in its initial problem. Although two other birds rapidly reached criterion in the transfer task (one macaw and one caique), neither demonstrated capacities that were superior to their initial performances. The spontaneous performance of one subject (Red) on the transfer task may therefore provide tentative evidence that parrots possess capacities to transfer learned information across novel tasks. Subjects also appear to retain learned information. When subjects were retested on ten trials of their original task, two of the four birds that reached criterion in the transfer task (one macaw and one caique) solved the problem without making any errors.

These experiments demonstrate that both macaws and caiques are capable (in some cases) of rapidly learning to solve a complicated means-end problem. Such performances suggest that parrots solve problems through trial-and-error associative learning; in which the affordances of a problem are revealed through repeated experience. Hence, because subjects repeatedly made errors before solving their initial task, it appears that solutions to such problems were initially achieved without any causal understanding of the relationships between the gaps and the cups. Subjects may therefore have learned to solve these initial problems by applying a procedural rule that was based on an arbitrary cue. Impressively however, when retested on their initial task, macaws and caiques could later recall this learned information. Such performances suggest that the formation and retention of learned procedural rules may be a particularly efficient approach to solving problems

within a task-specific context. The striking performance of at least one subject however, which spontaneously solved a novel transfer task that had no perceptual cues in common with the first task, suggests that parrots may also be capable of higher-order cognitive processing, such as rule abstraction. The transfer tasks were designed to preclude solutions from simple procedural rules that may have been learned during the initial task. Hence, it appears that at least one subject solved the transfer task by generalising previously learned principles about physical relationships between the cups and gaps across tasks. Yet only one of eight parrots demonstrated such capacities. While the ability to transfer conceptually learned information across novel problems might therefore be considered particularly challenging, the results from this study may also be constrained by a small sample size. Hence, such capacities may be broadly revealed in subsequent studies that incorporate a greater number of subjects.

5.3: General Discussion

By presenting non tool-using species with tasks that do not require an ability to use tools, but which require an understanding of the physical relationships between objects, it may be possible to reveal whether physical cognition has evolved as an adaptive specialisation that is restricted to tool-using species, or whether physical cognition may be a domain general trait that is shared among species that possess relatively large brains. However, many of the more subtle intricacies of means-end comprehension in birds may be overlooked when interpreting the more elaborate aspects of folk physics. Although means-end tasks have been presented to numerous species of birds, they were initially designed to assess physical cognition in tool-using primates (Klüver, 1933, Köhler, 1927). Hence, success on such tasks in non tool-using species of birds may reveal a suite of causal mechanisms that have previously been established in primates. For example, it should not be taken lightly that birds are capable of understanding the concepts involved

when pulling a string and retrieving a reward. Subjects must discriminate between lids that are either attached or disconnected to strings, understand that a reward resting in a lid can be retrieved by certain motor actions, and understand that the actions have to be directed towards the self for the food to move within reach. Such tasks may therefore be considered complex and challenging, even before assessing subjects' abilities to discriminate between connectivity and the size of lids or gaps that rewards have to pass through.

The findings presented here reveal that non-tool-using macaws and caiques both possess an ability to comprehend means-end object relationships. Furthermore, such capacities may be restricted to species that possess a relatively large brain size, suggesting that large brains confer capacities for sophisticated physical cognition. Results from the Connected problem reveal that subjects may possess a spontaneous comprehension of connectivity, suggesting that macaws and caiques are capable of understanding the causal relationships between objects. While subjects performances on the Connected transfer problem were impaired by novel materials, results from the more challenging Trap-Gaps paradigm reveal that parrots may be capable of using previously learned information to solve subsequent problems through rule abstraction. Such results highlight the need to further investigate the cognitive mechanisms that underlie animal physical cognition.

Many species can successfully discriminate between vertical or horizontal materials that are connected or disconnected to rewards, or rewards that are resting on or off materials, for example; apes (Herrmann et al., 2008, Mulcahy et al., 2012, Povinelli, 2000), monkeys (Hauser et al., 1999, Hauser et al., 2002b), parrots (Auersperg et al., 2009, Krasheninnikova et al., 2013, Werdenich and Huber, 2006), ravens (Heinrich, 1995a) and elephants (Irie-Sugimoto et al., 2008). Few species, however, have demonstrated the ability to successfully solve a similar means-end task, the Trap-Table problem. In this task, subjects are required to rake in a reward while avoiding a trapping hole. Hence, like the means end connected problem, subjects must attend to a continuous and discontinuous surface. One in six chimpanzees successfully

solved this problem in two 10 trial sessions (Povinelli, 2000, p. 137). Hoolock gibbons (*Hylobates hoolock*) also solved the Trap-Table problem, with one subject performing successfully from the first trial (Cunningham et al. 2006). However, subjects in the above studies were initially provided with training on a Trap-Table without a trap. Hence, the successful individuals may have solved the problem not through a causal understanding of traps, but due to a learnt association between the reward and the continuous surface (a similar limitation to the findings for the means-end Connected problem in Section 5.1 and also Auersperg's (2009) study). While vervet monkeys (*Cercopithecus aethiops*) showed some comprehension of the problem, selecting the correct no-trap surface on 65% of trials (Santos et al., 2006), capuchin (Fujita et al., 2003) and tamarin monkeys (Santos et al., 2006) failed to solve the Trap-Table problem. However, when provided with a single tool, 20 out of 24 apes avoided the trap on the first trial, suggesting that they may be sensitive to the causal relationships of the task (Girndt et al., 2008). Although it was not clear whether the apes in this study had a natural tendency to avoid holes.

While subjects may eventually solve such complex problems by trial-and-error learning, the ability to transfer learned information across tasks may be particularly challenging. None of the macaws or caiques in the current study successfully transferred from familiar to novel materials in the Connected problem. Moreover, only one of eight successfully transferred learned information to spontaneously solve the Trap-Gaps problem. Mixed results have also been reported for similar studies in other species. A similar problem to the Trap-Table task is the Trap-Tube task (Seed et al., 2006). While seven of eight rooks rapidly solved the Trap-Tube task, only one rook demonstrated capacities to understand the causal principles underlying the traps by solving a series of transfer tasks that had no visual cues in common (Seed et al., 2006). Chimpanzees have also demonstrated capacities to solve this problem when allowed to move the reward with their fingers (Seed et al., 2009b). However, numerous species of parrots have previously failed to avoid the traps in this task (Liedtke et al., 2010).

Due to the functional similarities of the Trap-Tube and Trap-Table tasks, these problems have also been used to assess the ability to transfer learned information across both tasks. After initially learning to solve either a Trap-Tube or Trap-Table problem, great apes, however, failed to successfully generalise learned information when presented with the corresponding novel, but functionally similar transfer task (Martin-Ordas et al., 2008). In contrast, three of six New Caledonian crows, revealed capacities to solve a Trap-Tube problem, based on an understanding of causal principles (Taylor et al., 2009). Furthermore, these successful birds also solved a Trap-Table transfer task within 20 trials, whereas the birds that failed to solve the Trap-Tube task also failed the Trap-Table task. In a similar study involving Traps and Barriers, apes received prior experience with either a Barrier or Trap platform, or a non-obstacle platform (Martin-Ordas et al., 2012). When presented with subsequent Barrier or Trap transfer problems, apes that had previously experienced obstacle platforms outperformed those subjects that initially received the non-obstacle platform (Martin-Ordas et al., 2012). Together, these findings suggest that rooks (Seed et al., 2006), New Caledonian crows (Taylor et al., 2009), apes (Martin-Ordas et al., 2012, Seed et al., 2009b), as well as caiques and possibly macaws, possess capacities to solve sophisticated problems by generalising learned information across novel transfer tasks. Such mechanisms may account for the flexible behaviours observed in these species, which may result in a domain general intelligence that is shared among relatively large brained species.

Chapter 6: Serial Reversal Learning and the Evolution of Behavioural Flexibility

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6.0.1: Abstract

Serial reversal learning of colour discriminations was assessed as an index of behavioural flexibility in two captive species of Neotropical parrots. Both species improved their performances with experience, but no between-species differences were observed, suggesting similar capacities for flexible responses to the alternating reward contingencies. In a second task, the mechanisms behind serial reversal learning in parrots were investigated, by comparing subjects' performances at a low or high pre-reversal training criterion. If reversals are solved through processes of associative learning, a high pre-reversal training criterion is expected to strengthen learned associations and hence impede post-reversal performances. However, highly reinforced associations may alternatively be used to generate conditional rules that can be generalised across reversals problems, thus rapidly improving post-reversal performances. I found that high criterion subjects made fewer post-reversal errors than low criterion subjects. Red-shouldered macaws and black-headed caiques therefore demonstrate capacities for solving reversal problems by applying conditional rules, hence demonstrating cognitive, rather than associative, modes of learning. Such performances coincide with findings in great apes, but contrast with findings in monkeys and prosimians, which generally show impaired reversal performances when trained to a highly rigorous pre-reversal criterion. Overall, these findings provide empirical support for an evolutionary convergence of behavioural flexibility between parrots and non-human great apes. Behavioural flexibility may therefore be related to similar socio-ecological variables shared among these families.

6.0.2: Introduction

While the behaviours of some animals appear to be restricted by inflexible stimulus-response action patterns, other animals appear to possess an ability to respond flexibly to environmental stimuli by generalising learned information to novel situations. For example, corvids (blue jays, rooks, jackdaws, and Eurasian jays), monkeys and apes, appear to extract general rules to rapidly solve a series of novel, but functionally identical discrimination problems, whereas pigeons slowly learn each novel discrimination problem anew, suggesting an inability to transfer previous learned information across similar problems (Hunter and Kamil, 1971, Wilson et al., 1985). Hence, the ability to transfer abstract information across problems appears characteristic of certain species, possibly because it is cognitively demanding. Behavioural flexibility has therefore been considered as one of the cognitive tools that are shared among species which possess particularly large relative brain sizes, such as apes, corvids and possibly parrots (Emery and Clayton, 2004a).

Among the methods used to compare behavioural flexibility across species is serial reversal learning, as success on this task requires an ability to flexibly respond to a fixed set of stimuli with a fluctuating reward regimen (Bond et al., 2007). Serial reversal learning typically requires subjects to make a binary choice discrimination between one colour, which is repeatedly rewarded and another colour, which is not. Subjects eventually learn to discriminate between the rewarded and non-rewarded colours, after which the reward contingencies are reversed (i.e. A+B- becomes A-B+). Reversed contingencies therefore require subjects to inhibit responses to previously learned associations and re-learn each new association using potentially conflicting information. Subjects initially require many trials to successfully respond to reversals, but may improve their performances with experience. However, as there are no cues to predict when the contingencies have been reversed, subjects will make at least one error after each reversal. Hence, an optimal performance may eventually be achieved on the second post-reversal trial. To do this, subjects have to adopt a *win stay-lose shift* rule: always try

the response that was last rewarded, and if that is no longer rewarded, shift to the other response, otherwise stay (Levine, 1959, Levine, 1965). Animals may therefore use their previous experience to develop conditional rules that enable them to rapidly switch between contingencies; demonstrating an ability to generalise information across reversal problems (Bond et al., 2007, Day et al., 1999).

Performances on reversal learning tasks have previously been used to quantify differences in learning across a wide variety of species (Bitterman, 1965). Yet distantly related species possess dramatically different perceptual, motivational and morphological traits, which can make direct comparisons of their cognitive traits difficult to interpret (Bitterman, 1960, 1965, 1975, Breland and Breland, 1961, Macphail, 1982, Warren, 1965, Tomasello and Call, 1997). One approach that attempts to alleviate such concerns is the comparative method (Harvey and Pagel, 1991). Closely related species may be expected to share similar physiological and cognitive traits as a result of common descent. Hence, by comparing closely related species that differ in certain socio-ecological aspects, any cognitive divergences can be attributed to contrasts in a species ecology or life history (Balda et al., 1996, Bond et al., 2003, 2007, Day et al., 1999). Bond and colleagues (2003, 2007), for example, used the comparative method to reveal that increased sociality among corvids predicts aptitude on a number of cognitive tests; including serial reversal learning. Another approach that has been applied specifically to serial reversal learning paradigms to reduce the confounds of interspecific differences in perception, manual dexterity and motivation, among primates, is to standardise each species' pre-reversal acquisition performances (Rumbaugh and Pate, 1984b). That is, initially training subjects to a certain level of correct choices, irrespective of the number of trials that it takes to do so, and then comparing subjects' immediate performances after the contingencies have been reversed. Thus, the structural relationships of animal intelligence are assessed rather than making direct comparisons based on the absolute number of trials that each species requires to solve a certain problem (Bitterman, 1960, Mackintosh, 1988).

The extent of pre-reversal training, however, also appears to have contrasting influences on the post-reversal performances of different species. Prosimians and monkeys, for example, tend to show impaired post-reversal performances when trained to a rigorous pre-reversal criterion of 84% correct choices, but enhanced post-reversal performances when trained to a low pre-reversal criterion of 67% correct choices (Rumbaugh and Pate, 1984b). Conversely, apes show enhanced performances when trained to a high pre-reversal criterion and impaired post-reversal performances when trained to a low criterion (Rumbaugh and Pate, 1984b).

The impaired post-reversal performances of prosimians and monkeys when presented with a high, rather than low, pre-reversal criterion reveals that as the strength of the learned associations increases, the ability of these species to inhibit responses to previously learned associations decreases (De Lillo and Visalberghi, 1994, Rumbaugh and Pate, 1984a, 1984b). This is because each previously learned association must first be extinguished and then each new association re-learned. Consequently, prosimians and monkeys are considered to solve serial reversal problems through associative processes of repeated conditioning and extinction (De Lillo and Visalberghi, 1994, Rumbaugh, 1970, Rumbaugh and Pate, 1984b). Mixed results have however been reported for rhesus monkeys (Essock-Vitale, 1978, Washburn and Rumbaugh, 1991) and capuchin monkeys (Rumbaugh, 1970) subjected to different testing procedures; although recent studies place capuchin performances among those of other monkeys rather than apes (Beren et al., 2008, De Lillo and Visalberghi, 1994).

Apes, on the contrary, perform better on post-reversal trials when they are presented with a high, rather than low, pre-reversal learning criterion (Essock-Vitale, 1978, Rumbaugh and Pate, 1984a, 1984b). Animals that quickly adjust to reversed contingencies can only do so by understanding the underlying principles of serial reversals (Shettleworth, 2010). Apes may therefore develop a *win stay–lose shift* rule in response to alternating contingencies when subjected to a high learning criterion, but fail to extract this information

when presented with a low pre-reversal criterion. Apes are therefore considered to demonstrate higher-order learning, as they mediate their post-reversal responses by means of their pre-reversal experience; hence transferring conditional rules across reversals (Rumbaugh and Pate, 1984a, 1984b).

Such qualitative differences in learning processes among primates suggest that the ability to generalise conditional rules across reversal tasks may be cognitively demanding as it appears restricted to larger-brained species, such as apes (Rumbaugh, 1971). Although I am not aware of any studies that have investigated the serial reversal learning performances of parrots or corvids using high and low pre-reversal criteria, evidence suggests that both families demonstrate flexibility on similar paradigms. Red-billed blue magpies and Yellow-crowned Amazon parrots, for instance, outperformed White Leghorn chickens, and Bob White quail on serial reversals of a spatial discrimination problem (Gossette et al., 1966). Corvids, but not pigeons, also demonstrate abilities to solve problems that require the abstraction of a general rule across a change of stimuli, such as matching or oddity discriminations (Wilson et al., 1985) and learning-set problems (Mackintosh, 1988). Corvids also demonstrate an ability to positively transfer learned rules between colour and spatial serial reversal problems (Bond et al., 2007), and can transfer learned information from successive reversals to better solve learning set problems by applying a *win stay–lose shift* strategy (Kamil et al., 1977). Such findings suggest that parrots and corvids, along with apes, demonstrate similar generalised learning strategies and flexible behaviour.

The aim of this study is to determine whether two species of Neotropical parrots are capable of generating flexible behaviours in response to a serial reversal-learning paradigm. Parrots are a particularly attractive species for investigating such questions as they share with apes and corvids many of the socio-ecological precursors associated with complex cognition, such as a relatively large brain size, manual dexterity, extractive foraging, longevity and

a large, multi-layered social organisation (van Horik and Emery, 2011, van Horik et al., 2012).

Two experiments are reported in the current study. In the first experiment, red-shouldered macaws and black-headed caiques were presented with a serial reversal learning task and between-species performances were compared as a suggested index of behavioural flexibility (Bond et al., 2007). As both species possess a similar relative brain size, and live in complex social groups, we may expect red-shouldered macaws and black-headed caiques to demonstrate similar responses to the alternating contingencies. However, between-species differences may also be predicted based on the contrasting selection pressures that each species may experience due to differences in their natural habitats.

A second experiment was also designed to reveal the psychological mechanisms underlying reversal learning in parrots. Here two alternative hypotheses are addressed: (1) that parrots only solve reversal problems through processes of associative learning and conditioning; and (2) that parrots are capable of transferring a conditional rule across serial reversal discrimination problems, and may therefore use cognitive, rather than associative mechanisms to solve such tasks.

6.0.3: General Methods

Apparatus and Training

Two 6 cm diameter plastic lids, of different colours (depending on the experiment), were attached to a wooden base (28 cm x 7 cm), and separated by 12 cm. Both lids were fixed to hinges and could be manipulated to reveal a concealed food reward of crushed Lafeber Nutri-Berries (Figure 6.1). The apparatus was initially presented to subjects without lids and with one food-

well containing food. After subjects fed from the apparatus without hesitation, an orange lid was fixed to each of the baited food wells, again with only one well baited. To proceed to test, subjects were required to retrieve the concealed food by opening the lids at least ten times in one 10min session.

Procedure

Subjects were not food deprived, although testing was conducted in the morning prior to their regular feeding schedule. Each subject was provided with one session of 10 trials per day. The presentation of rewarded and unrewarded coloured lids was counterbalanced and randomly assigned across subjects. To prevent the development of side biases, the position of the lids (i.e. left or right hand side presentation) was pseudo-randomised within sessions so that the lids did not occur on the same side for more than two consecutive trials. Each subject was tested individually in a familiar but visually isolated enclosure. During testing days, all subjects participated in the experiment. During trials, the experimenter attempted to avoid providing subjects with any inadvertent cues to the location of the concealed reward by holding and presenting the apparatus in a symmetrical fashion and then placing his hands behind his back and looking only at the centre of the apparatus. Subjects were allowed to upturn one lid per trial and were considered to have made a correct choice if they chose the baited lid. If subjects upturned the correct lid, they were allowed to retrieve the food reward. However, if subjects upturned the un-baited lid, then the apparatus was immediately removed. If subjects failed to retrieve the baited lid on one trial, the succeeding trials followed the predetermined pseudorandomised order. The apparatus was re-baited out of view of the subject. Subjects that chose the same side over six consecutive trials in one block were considered to have developed a side bias. To correct for side biases, I presented the baited lid on the non-preferred side until the subject chose the baited side for two consecutive trials. Trials then reverted to the original pseudo-randomised configuration. Corrected and non-corrected trials were combined for analysis. I recorded all trials with a digital camcorder (JVC Everio, Model No. GZ-

MG645BEK, Malaysia) and scored the number of errors to reach criterion for each reversal.

Data Analysis

All data were assessed with Shapiro-Wilk's and Levene's tests and met assumptions of normality and homogeneity of variance for parametric analysis. Between-species comparisons of the number of trials to reach the initial colour association (CA) criterion were assessed using Independent t-tests. The number of trials to reach the CA and first reversal (R1) criterion in Experiment 1 were compared with a paired t-test. The number of trials to reach the CA criteria for the High and Low groups were compared using an independent t-test. As any effects of extinction were expected to be most prominent in the initial post-reversal trials (Bond et al., 2007), between-species differences in errors for the first 10 post-reversal trials across subsequent reversals were assessed with a Repeated measures ANOVA. Planned within subjects' comparisons were performed using Paired t-tests. All analyses were two-tailed and conducted in SPSS (SPSS for Mac OS X, 2007).

6.1: Between-species Comparisons of Serial Reversal Learning Performances

6.1.1: Methods

Apparatus

The same apparatus as the training sessions was used but with novel coloured lids, one green and one blue (Figure 6.1).

Procedure

Subjects were presented with one block of 10 trials per day. Once subjects reached a predetermined criterion of seven consecutive correct trials in one block of 10 trials (significant according to a binomial test with a probability of choosing either side set at 0.5), they were immediately presented with a block of 10 trials with reversed contingencies (i.e. S+ becomes S-). Each subject was presented with as many blocks as required to reach eight serial reversals.

6.1.2: Results

There were no significant differences in the total number of trials that each subject participated in, between macaws (mean = 503.75 ± 67.38 SEM) and caiques (mean = 554.75 ± 47.46 SEM): Independent t-test; $t = 0.619$, $df = 6$, $p = 0.559$. No between-species differences in the number of trials to reach criterion were revealed for the initial CA trials (Figure 6.2); Independent t-test; $t = 1.817$, $df = 6$, $p = 0.119$, (macaws mean = 28 ± 3.94 SEM; caiques mean = 41 ± 5.97 SEM). However, these findings are constrained a low sample size (Observed Power = 0.33), suggesting that a significant result may be revealed with additional subjects. Macaws may therefore have reached CA criterion in significantly fewer trials than caiques if more subjects participated in this study. The number of initial post-reversal blocks where subjects developed a side bias were as follows (R1 represents the first reversal; R8 represents the last reversal): Macaws; No.2 (R1), No.4 (R7, R8), No.5 (R5), No.8 (R2, R6, R7), Caiques; Green (R2, R4, R6), Gold (R5), Purple (R5, R6, R8), Red (R3, R6).

Because there were no significant between-species differences in the number of trials to reach the CA criterion, subjects were pooled and the cumulative number of trials to reach CA (mean = 34.5 ± 4.12 SEM) and R1 criterion

(mean = 67.75 ± 7.80 SEM) were compared. Subjects reached criterion with significantly fewer trials in the initial CA condition than compared to the R1 condition (Figure 6.2); Paired t-test, $t = 3.567$, $df = 7$, $p = 0.009$.

Analysis of the number of errors in the first 10 post-reversal trials across serial reversals (R1-R8) showed no significant effect of species (Figure 6.3); Repeated measures ANOVA, $F_{1,6} = 2.647$, $p = 0.155$, and no significant reversal x species interaction; Repeated measures ANOVA, $F_{7,42} = 1.874$, $p = 0.098$, suggesting that both species' serial reversal performances were similar (Figure 6.3).

There was however a significant within subjects effect of reversal (Figure 6.3); Repeated measures ANOVA, $F_{7,42} = 2.550$, $p = 0.028$, although a planned within subjects comparison between the first reversal (R1; mean = 7.63 ± 0.67 SEM) and the last reversal (R8; mean = 6.50 ± 0.45 SEM) did not reveal any significant differences in errors; Paired t-test, $t = 1.468$, $df = 7$, $p = 0.185$, suggesting that subjects performances may have improved, but not consistently with experience.

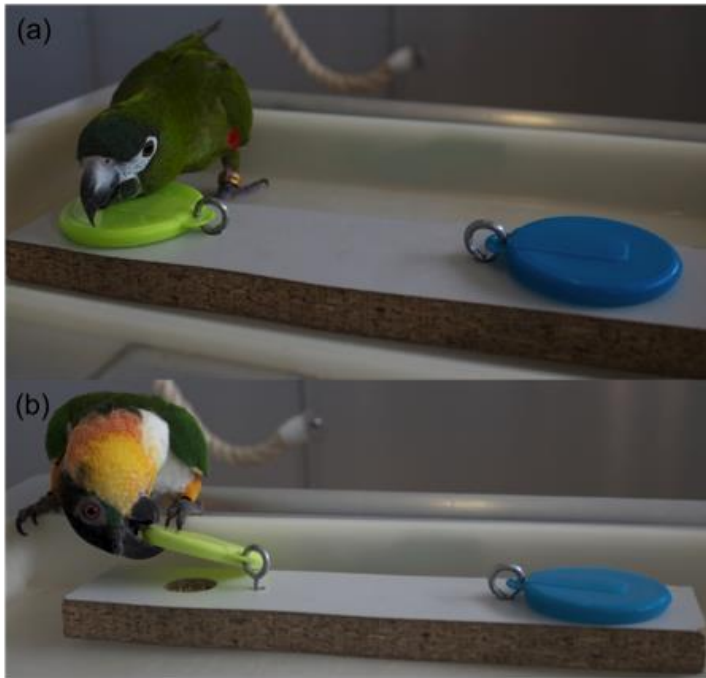


Figure 6.1: (a) a red-shouldered macaw and (b) a black-headed caique performing a discrimination trial on the Serial Reversal Learning apparatus.

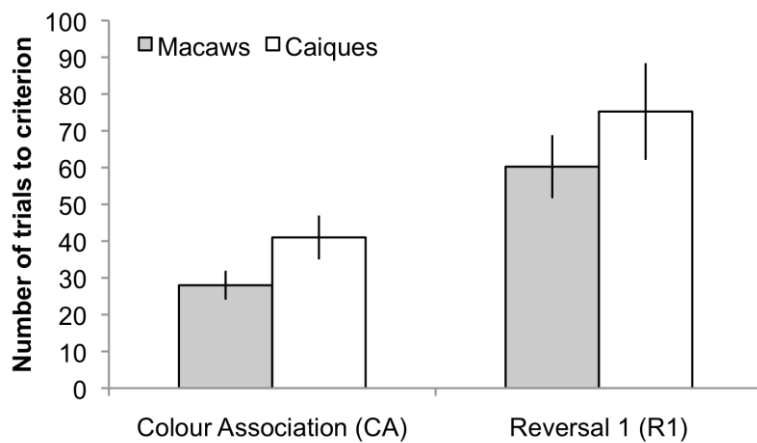


Figure 6.2: Experiment 1. Mean number of trials (\pm SEM) to reach reversal criterion for the colour association (CA) and first reversal (R1) conditions, for macaws and caiques.

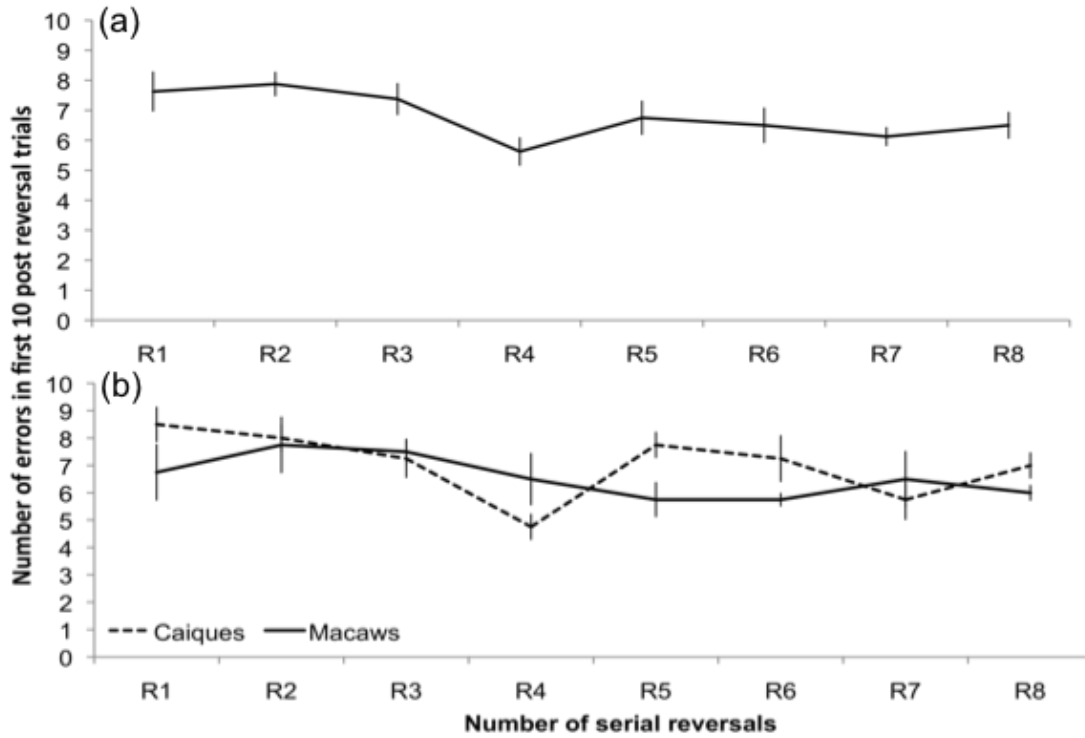


Figure 6.3: Experiment 1. Mean number of errors (\pm SEM) for (a) pooled subjects and (b) macaws and caiques, for the first 10 post reversal trials across eight successive colour reversals (R1-R8).

6.1.3: Discussion

In Experiment 1, the serial reversal learning performances of two species of parrots were compared as a suggested index of behavioural flexibility (Bond et al., 2007). Both species showed comparable performances during the CA trials and across eight serial reversals. Although there were no statistical differences in reversal performances between species, macaws generally required fewer trials than caiques to reach criterion during the initial CA trials. Any between-species differences may have therefore been revealed by using a larger sample size. Both species, however, required more trials to reach criterion during first reversal than compared to the CA problem. These findings suggest that previously learned associations initially impaired subjects' reversal performances. Both species therefore required trial and error experience of the reversed contingencies to first extinguish the previously learned associations and then re-learn each following association anew.

Although subjects' performances between the first and last reversals (R1 and R8) were similar, a within subjects improvement in errors across reversals was revealed, suggesting that macaws and caiques may use their previous reversal experience to mediate their subsequent responses. These findings correspond with those of previous studies, where the ability to rapidly recover from reversed contingencies has been interpreted as an index of behavioural flexibility (Bond et al., 2007, Day et al., 1999).

To further investigate behavioural flexibility in parrots, I presented subjects with a second experiment that was designed to reveal the psychological mechanisms underlying reversal learning. As no between-species differences in reversal learning performances were observed, I decided to pool subjects and randomly assign individuals from both species into one of two conditions that required either a high or low learning criterion of successful discriminations prior to each reversal. High criterion subjects were therefore exposed to a more rigorous pairing of the colour associations and hence were

expected to be confronted with greater interference during their post-reversal trials; requiring a greater number of trials to extinguish and then re-learn each new contingency. By contrast, subjects exposed to a low criterion were provided with the minimal number of trials required to reach binomial significance, and therefore are expected to experience less interference during post-reversal trials.

Hence, if parrots only use associative learning to solve each reversal problem, then I predict subjects in the high criterion condition to make more errors than low criterion subjects. Conversely, if subjects in the high criterion condition solve post-reversals with fewer errors than low criterion subjects, then there must be some transfer of abstract information across reversals.

6.2: The Mechanisms Underlying Serial Reversal Learning

6.2.1: Methods

Subjects, Apparatus and Training

The same subjects and general procedures as in Experiment 1 were used, however, in this experiment novel coloured lids; either pink with a green circle sticker, or yellow with orange circle sticker were introduced. The colour of the rewarded lids was counterbalanced across subjects.

Procedure

As no between-species differences were observed in Experiment 1, subjects were pooled and individuals from each species were randomly assigned into either High or Low Criterion conditions. Each session consisted of up to 20 trials.

The High Criterion group (No.4, No.5, Green & Red) were presented with reversals once they scored at least 19/20 correct choices in one 20 trial session. Conversely, the Low Criterion group (No.2, No.8, Gold & Purple) were presented with reversals once they achieved either: 15 correct choices in one 20 trial session, 7 consecutive correct choices in the first 10 trials of one session, 9/10 correct choices in either the first or last 10 trials of a 20 trial session, or 10 consecutive correct choices within one 20 trial session. The Low Criterion group included a number of different pre-reversal criteria to ensure that the number of trials subjects required to reach each learned association was minimised and hence subjects were not over-trained. All criteria were significant according to a binomial test, with a probability of choosing either side set at 0.5, and alpha set at 0.05. Subjects were presented with as many trials as required to reach 11 reversals.

If subjects reached criterion within one 20 trial session, they were immediately presented with one reversal session. On two occasions, subjects (No.8 and Gold) reached a second criterion within their first post-reversal session. On these occasions I did not provide a further post-reversal session and resumed testing on the following day. Subjects were therefore presented with up to a maximum of 40 trials per day. These procedures attempted to maintain motivation by prohibiting subjects from becoming satiated on rewards. Side biases were corrected for, and included in the analysis as in Experiment 1. I ceased testing individual subjects once they had participated in 11 reversals. All trials were coded live but digitally recorded for subsequent analysis if required.

6.2.2: Results

There were no significant differences in the total number of trials that each subject participated in, between Low (mean = 744.75 ± 24.87 SEM) and High (mean = 695 ± 28.72 SEM) Criterion groups: Independent t-test; $t = 1.309$, df

= 6, $p = 0.238$. There were no significant differences in the number of trials to reach criterion for the initial CA trials between Low Criterion (mean = 72.75 ± 23.86 SEM) and High Criterion groups (mean = 75 ± 9.57 SEM; Figure 6.4); Independent t-test; $t = 0.088$, $df = 6$, $p = 0.933$. The number of initial blocks where subjects developed a side bias are as follows: High Criterion; No.4 (R4, R10), No.5 (R4, R5), Green (R6), Red (R1), Low Criterion; No.2 (R3), No.8 (R1, R2, R7, R10, R11), Gold (R4, R5, R9, R10, R11), Purple (R2, R3, R7, R10, R11).

Analysis of errors in the first 10 post reversal trials across successive reversals (R1-R11) showed a significant effect of condition, with the High Criterion group making fewer errors in the first 10 post reversal trials across successive reversals than the Low Criterion group (Fig. 6.5); Repeated measures ANOVA, $F_{1, 6} = 23.133$, $p = 0.003$. There was no significant reversal x criterion interaction; Repeated measures ANOVA, $F_{10, 60} = 1.635$, $p = 0.119$.

There was however a significant within-subjects effect of reversal; Repeated measures ANOVA, $F_{10, 60} = 4.404$, $p < 0.001$. A planned comparison of R1 and R11 performances revealed a significant reduction in errors across reversals for the High Criterion group (R1 mean = 7.75 ± 0.95 ; R11 = mean 3 ± 0.00 SEM); Paired t-test, $t = 5.019$, $df = 3$, $p = 0.015$, but not for the Low Criterion group (R1 mean = 7.75 ± 0.75 ; R11 mean = 5.75 ± 0.48 SEM); Paired t-test, $t = 2.449$, $df = 3$, $p = 0.092$.

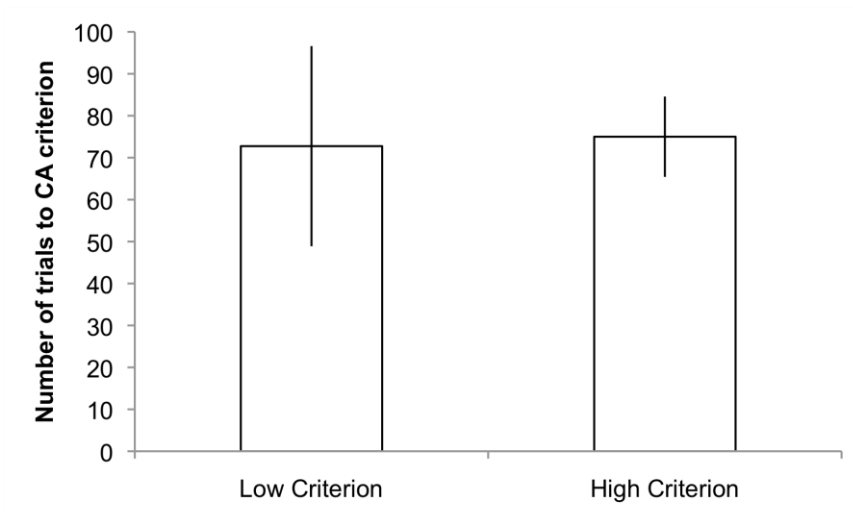


Figure 6.4: Experiment 2. Mean number of trials (\pm SEM) to reach criterion for the Colour Association (CA) task, for High Criterion and Low Criterion conditions.

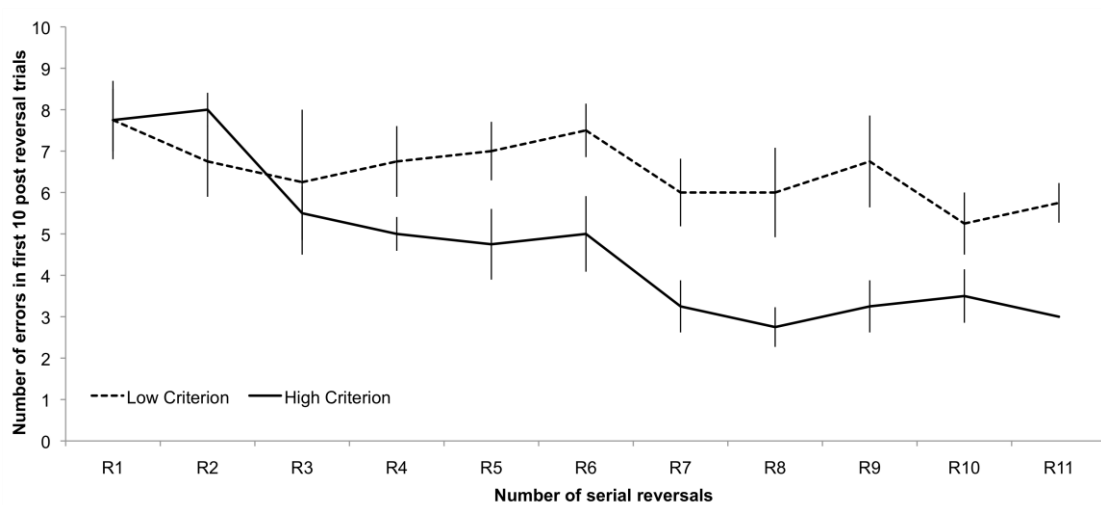


Figure 6.5: Experiment 2. Mean number of errors (\pm SEM) for the first 10 post reversal trials across eleven successive colour reversals (R1-R11), for Low and High Criterion conditions.

6.2.3: Discussion

In Experiment 2, the psychological mechanisms underlying reversal learning in parrots were investigated. As there were no between-species differences in reversal performances in Experiment 1, all subjects were pooled and randomly assigned to either High or Low Criterion groups. Subjects in the High Criterion group made fewer post-reversal errors than subjects in the Low Criterion group. The High Criterion group thus improved their performances across subsequent reversals, whereas there was no apparent effect of learning for subjects in the Low Criterion group.

It therefore appears that the High Criterion group used the enhanced associative strength of the learned contingencies to generate a conditional *win stay–lose shift* rule to rapidly respond to subsequent reversals. The Low Criterion group on the other hand, failed to generate such concepts and hence required a greater number of trials to first extinguish the previously learned associations and then re-learn new discriminations through processes of conditioning. Overall, these results support our second hypothesis; that parrots are capable of transferring learned information across serial reversal discrimination problems, and may therefore use higher order cognitive mechanisms, such as rule abstraction, to flexibly solve such tasks.

6.3: General Discussion

Two main conclusions can be drawn from these results. The first is that macaws and caiques appear to show similar capacities to respond to alternating contingencies in a serial reversal learning task, and hence behavioural flexibility. Second, it appears that parrots, like corvids and apes, differ from pigeons, monkeys and prosimians in their ability to generate conditional rules to flexibly solve reversal problems.

Subjects trained to low pre-reversal criteria showed no improvements in their performances across reversals. When presented with reversed contingencies, each previously learned association required a number of trials before it was lost through extinction. Each new association then required further trials to re-learn through conditioning. Hence, at a low criterion, reversed contingencies appeared to be learned through associative processes. Conversely, when presented with a high pre-reversal criterion, subjects made fewer post-reversal errors across successive reversals. Rather than being impaired by the increased strength of the conditioned associations, subjects rapidly learned to respond to the alternating contingencies. Such findings suggest that parrots may understand the conditional principles underlying serial reversals. These results are also consistent with reversal performances of other large-brained species, such as the great apes; in contrast to monkeys and prosimians (Essock-Vitale, 1978, Rumbaugh and Pate, 1984a, 1984b), suggesting that the ability to rapidly respond to serial reversals when trained to a highly rigorous pre-reversal learning criterion may be a trait shared among species with particularly large brains.

Rumbaugh (1995) argues that great apes, because of their ability to transfer abstract information across reversal tasks, are capable of mediating their behaviour through more cognitively demanding modes of learning than monkeys and prosimians. Such findings also correspond with species' encephalisation coefficients (Jerison, 1973, Rumbaugh and Pate, 1984b), suggesting a link between relative brain size and behavioural flexibility. Further evidence of generalised learning strategies, demonstrated by the positive transfer of information across serial reversal or learning set tasks involving disparate stimulus dimensions (i.e. space and colour), also support our findings. For example, chimpanzees and a number of species of macaques (reviewed in Macphail, 1982) and corvids (Bond et al., 2007, Gossette et al., 1966, Kamil et al., 1977, Mackintosh, 1988, Wilson et al., 1985) rapidly develop generalised learning strategies, whereas rats, cats, and pigeons do not (Durlach and Mackintosh, 1986, Macintosh et al., 1968, MacKintosh and Holgate, 1969, Warren, 1966). More recently however,

pigeons have been shown to adopt a *win stay–lose shift* rule when presented with a midsession reversal task involving short inter-trial intervals (Rayburn-Reeves et al., 2013); although short inter-trial intervals have long been recognised to enhance serial reversal learning performances (Stretch et al., 1964).

It is possible, albeit unlikely, that the High Criterion group produced fewer post reversal errors due to an Overtraining Reversal Effect (ORE). First observed by Reid (1953), the ORE is a phenomenon where overtraining on discrimination problems enhances post-reversal performances. Reid (1953) presented rats with a black-white discrimination problem in a Y maze. All of the rats were initially trained to a specific criterion, and then separated into three conditions depending on the amount of their post-criterion training. Rats exposed to increasingly rigorous training regimes made fewer post-reversal errors. Such findings are considered paradoxical as overtraining, according to classical learning theory, is predicted to increase the excitatory strength of S+ and inhibitory strength of S– and thus impede extinction when contingencies are reversed (Hull, 1943, Spence, 1956). Although ORE is commonly observed in rat studies, it is rarely reported in monkeys (Essock-Vitale, 1978, Sutherland and Mackintosh, 1971), with the exception of one account from stump-tailed macaques (Schrier, 1974). Typically, when presented with increasing numbers of acquisition trials, monkeys show impaired post reversal performances and do not improve with subsequent experience. Like monkeys, overtraining has also been reported to impair reversal performances in birds, such as myna (Gossette, 1969), chicks (Mackintosh, 1965, Warren et al., 1960), pigeons and Japanese quail (Gonzalez et al., 1966), suggesting that in these species, the ability to learn each new contingency is governed by processes of association and extinction. However, it has been suggested that post-reversal performances typical of an ORE should not only be highest following overtraining, but that performances on early post-reversal trials should also be lowest following overtraining (Sutherland and Mackintosh, 1971, pp. 258-261). Hence, in contrast to monkeys and the aforementioned species of birds, the improved

performances of great apes when presented with high training criteria are not considered typical of an ORE as high criteria facilitate apes' performances during both early and late post-reversal trials (Essock-Vitale, 1978). In the current study, subjects in the High Criterion condition showed a significant reduction in errors across subsequent reversals, while subjects in the Low Criterion condition did not improve their performances. If these findings were due to an ORE, we might also expect subjects in the High Criterion condition to perform significantly worse than Low Criterion subjects during initial reversals. However, performances on the first 10 post-reversal trials across the first three reversals were comparable for both Low and High Criterion subjects (see R1-R3; Figure 6.5), revealing that subjects were not initially impaired by the different reversal criteria. These findings therefore suggest that subjects' performances in the High Criterion condition were unlikely to be a result of an ORE.

The performances of parrots in the High Criterion condition also appear to support a relationship between brain size and behavioural flexibility, suggesting that large brains afford a selective advantage when responding to unusual, novel or complex socio-ecological challenges. For instance, large brains may provide a foundation for novel or altered behaviours, which may be applied to solve an array of problems through domain general cognitive processes (Sol, 2009). Moreover, the rationale that relatively large brains are found across phylogenetically distinct species, suggests that certain cognitive traits may have evolved independently among several vertebrate groups that share similar socio-ecological selection pressures (van Horik et al., 2012).

Indeed brain size appears to be a good proxy for the ability of species to flexibly respond to environmental change and hence fluctuations in resource abundance. As such, brain size positively correlates with the ability of species to accommodate habitat change (Shultz et al., 2005), climatic change (Schuck-Paim et al., 2008), invade novel environments (Sol and Lefebvre, 2000, Sol et al., 2002, 2005, 2007, 2008) and generate innovative foraging behaviours (Lefebvre et al., 2004, 1997, Reader and Laland, 2002). Hence,

large brains may be particularly advantageous in complex environments or habitats that are novel or likely to change.

Given that red-shouldered macaws and black-headed caiques naturally inhabit contrasting environments (Juniper and Parr, 2003), such differences do not appear to have resulted in any obvious divergences in their abilities to respond flexibly to a serial reversal paradigm. Both macaws and caiques, however, possess a similar relative brain size (Iwaniuk et al., 2005), and share a complex social organisation characterised by long-term pair bonded relationships and fission-fusion foraging groups (Juniper and Parr, 2003). Similarities in the complexity of their social relationships, rather than habitat or foraging niche, may therefore promote behavioural flexibility in these species.

Social complexity has long been considered to play an important role in the evolution of a flexible and intelligent mind (Social Intelligence Hypothesis: Humphrey, 1976), with social group size and neocortex size corresponding positively in primates (Dunbar, 1998), ungulates (Shultz and Dunbar, 2006) and cetaceans (Marino, 1996). Brain size, however, also correlates positively in birds and mammals that form stable or pair-bonded relationships (Dunbar and Shultz, 2007, Emery et al., 2007, Shultz and Dunbar, 2007). Species that live in stable social groups, in contrast to more solitary or asocial species, may therefore develop particular cognitive adaptations to accommodate for the additional complexities that arise from maintaining relationships and interpreting others' behaviours. For example, primates that live in groups characterised by high fission-fusion social dynamics, demonstrate enhanced inhibitory control (another proposed index of behavioural flexibility), in contrast to species that live in more cohesive groups. Fission-fusion societies may therefore promote cognitive adaptations that result in greater behavioural flexibility; independent of phylogenetic relatedness or feeding ecology (Amici et al., 2008). Serial reversal learning also involves inhibitory control, as it requires an ability to restrain responses to previously reinforced stimuli, and instead flexibly direct behaviours towards potentially unrewarded alternatives. Hence, it has been suggested that serial reversal learning also bears

resemblance to the demands of a complex social system (Bond et al., 2007). Comparative research on corvids provides support for such suggestions by revealing that variation in serial reversal performances is best explained by social complexity, rather than ecological or spatial complexity (Bond et al., 2007). Certainly, the reversal learning performances among the two species of social parrots reported here appear to support such claims. Moreover, social corvids have been found to outperform more solitary corvid species on other cognitive tasks that require flexibility, such as transitive inference (Bond et al., 2003). Hence, social living may also promote cognitive adaptations that favour an individual's ability to interpret, predict and flexibly respond to the subtle intricacies of others' behaviours.

Although some socio-ecological contexts may be more influential than others, it is likely that there are a number of selection pressures acting on cognitive evolution. Yet familiar to each challenge is the construction of new or altered behavioural patterns (Sol, 2009). Behavioural flexibility may therefore represent a domain general trait that is shared among species that possess a relatively large brain size. Indeed, flexibility has been suggested as one of the fundamental cognitive tools that arose as a result of the evolution of complex cognition in corvids and apes (Emery and Clayton, 2004a). Overall, these findings provide further empirical support of an evolutionary convergence of behavioural flexibility between distantly related species that possess relatively large brains.

Chapter 7: General Conclusions

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7.1.0: General Conclusions

Despite many similarities in their biology, life histories and socio-ecology, red-shouldered macaws and black-headed caiques were found to display differences in their social dynamics (Chapter 2) and have contrasting propensities to interact with objects (Chapter 3). Macaws invest more time in affiliative behaviours, such as allopreening, and were observed to spend more time in social groups than compared to caiques. Conversely, caiques spent more time engaged in solitary behaviours but demonstrated relatively low levels of object neophobia and were highly explorative of objects. Such differences may correspond with particular socio-ecological selection pressures that each species experience in their contrasting natural environments. Macaws naturally inhabit open homogeneous wooded environments that are characterised by a stable supply of resources. Caiques by contrast inhabit dense, heterogeneous, closed canopy forest, in which the availability of particular resources may fluctuate more widely (Juniper and Parr, 2003, Mettke-Hofmann et al., 2002). Differences in each species' natural habitats may promote different socio-ecological selection pressures, which correspond with differences in behaviours. Macaws, for example, may invest more in affiliative behaviours, because an enhanced strength of pair-bonded relationships may be required to aid coordination and cooperation to raise offspring (Emery et al., 2007). Conversely, caiques may be particularly explorative of objects due to the requirements of adopting generalised foraging strategies that are necessary to acquire or extract food in their particular environment (Glickman and Sroges, 1966, Mettke-Hofmann et al., 2002, Webster and Lefebvre, 2000). However, as little is known about the behaviours of these species in the wild, such speculation must be interpreted cautiously. Without comparing a greater variety of species, it may also be difficult to interpret whether such behavioural differences are solely driven by differences in each species respective niches. Yet, irrespective of these behavioural and ecological differences, macaws and caiques demonstrated comparable performances on a series of tasks that assessed physical and social cognition, such as four innovative foraging tasks (Chapter 4), two means-ends reasoning tasks (Chapter 5) and two serial reversal learning

tasks (Chapter 6). Moreover, these species also reveal performances that are similar to other large-brained species of parrots, corvids and apes).

Different selection pressures are likely to correspond with particular adaptive specialisations to solve challenges that animals face within their respective environments (Shettleworth, 2010). A classic example of this is found among food-storing bird species that rely on maintaining a consistent supply of resources may benefit from adaptive specialisations that help enhance their foraging success (Clayton and Dickinson, 1998). Social or physical cognition may have therefore evolved as a domain specific adaptation to particular socio-ecological selection pressures that a common ancestor of parrots experienced. However, the contrasting life history traits of red-shouldered macaws and black-headed caiques do not appear to have influenced their abilities to solve a variety of cognitively demanding tasks. Hence, the notion that social cognition is enhanced in social species, or species that naturally use tools possess advanced physical cognition, may oversimplify such relationships. Adaptive specialisations can be flexible with respect to the current environmental conditions (Pravosudov and Clayton, 2001). Findings reported in this thesis suggest that advanced cognitive abilities may be generalised across social and physical domains, through processes of behavioural flexibility, and hence result in capacities for a domain general intelligence. Such results may complement findings from recent studies suggesting that the spontaneous and insightful comprehension of problems requiring an understanding of tools is not limited to species that naturally use tools in the wild (Auersperg et al., 2011, 2012, Bird and Emery, 2009a). The relatively large brain size of parrots and possibly corvids may have evolved in response to particular socio-ecological challenges. Such cognitive specialisations may allow animals to rapidly respond to a variety of domain specific problems through processes of behavioural flexibility. This ability to flexibly respond to a variety of challenges may then be extended across specific domains to afford capacities for a domain general intelligence (Emery and Clayton, 2004a).

7.1.1: Are innovative behaviours influenced by different propensities for object exploration & neophobia?

In Chapter 4, macaws and caiques revealed broad capacities to solve a series of innovative foraging problems. Both species rapidly learned to inhibit prepotent actions towards a clearly visible, but inaccessible food reward that was placed behind a clear Perspex barrier, and instead focussed their attention towards manipulating peripheral, but functional, components of the tasks. These findings suggest that parrots possess a degree of behavioural flexibility to overcome such problems. While all individuals from both species solved each task, there were no apparent between-species differences in the durations and types of functional or non-functional manipulations required to retrieve the rewards. However, as relative brain size and rates of innovative behaviours correlate positively among birds and primates (Lefebvre et al., 1997, 2002, 2004, Reader and Laland, 2002), macaws and caiques might be expected to show comparable performances due to their comparable, and relatively large, brain size (Iwaniuk et al., 2005).

This study reveals that capacities for innovative foraging behaviours, at least within these particular tasks and species, do not differ between two species of parrots that have contrasting predispositions to interact with objects (Chapter 3). Macaws are highly neophobic of objects, whereas caiques are highly explorative of objects. Yet, numerous studies suggest that neophobia inhibits innovative behaviours in animals in the wild, such as birds (Bouchard et al., 2007, Seferta et al., 2001, Webster and Lefebvre, 2000, 2001), primates (Day et al., 2003) and hyenas (Benson-Amram and Holekamp, 2012). However, findings from this study support the view that neophobia and neophilia may have little overall influence on innovative rates once animals become habituated to certain problems after repeated exposure (Benson-Amram et al., 2013). These findings also reveal that the mechanisms underlying innovative behaviours in individuals do not necessarily correspond with certain species-wide predispositions towards interacting with objects. For example, dietary generalists may be relatively more explorative of objects as a requirement of their natural foraging repertoires. Yet, findings reported here

suggest that dietary generalists and specialists, that possess a similar relative brain size, may reveal comparable propensities for innovative behaviours. One explanation that may account for the contrasting findings observed in this study, compared to the wild, is the natural frequency that animals are repeatedly exposed to novel objects. In the wild, neophobic animals may easily avoid repeated exposure to novelty. Animals confined to captivity, on the other hand, may not easily avoid such experiences. Hence, animals in captivity may habituate to novelty more rapidly, and therefore be more likely to interact with novel objects more frequently, than animals in the wild.

Although there were no obvious differences in innovative performances between individuals of different dominance ranks, an alternative explanation suggests that innovative behaviours are generated by certain motivational factors, such as a necessity to innovate to avoid competitive displacement from higher ranking individuals which dominate clumped resources (Thornton and Samson, 2012). Certainly low ranking caiques (Purple and Green) interacted with a greater variety of objects than high ranking caiques in a social setting (Chapter 3; 3.2). While the current study assessed solitary innovative behaviours, subsequent investigations that assess innovative behaviours in a controlled social setting may reveal further evidence to support such claims.

7.1.2: Do different propensities for object exploration influence an understanding of object relationships?

To investigate whether parrots are capable of comprehending physical object relationships, and whether different propensities for object exploration influence their understanding of object relationships, two Means-End tasks were presented to subjects (Chapter 5). The first Means-End task revealed that parrots could spontaneously pull strings and cloths to retrieve an otherwise out-of-reach reward. Moreover, parrots also showed spontaneous goal directed behaviours by discriminating between rewarded, rather than unrewarded materials. When using familiar materials, macaws and caiques

also discriminated between connected and disrupted problems. However, subjects' performances were impaired when they were presented with unfamiliar materials.

Macaws and caiques demonstrated comparable performances to other species of parrots (Auersperg et al., 2009) and apes (Herrmann et al., 2008, Mulcahy et al., 2012) on these initial tasks. Yet their performances on a transfer task were relatively poor in comparison to those of apes, which could successfully solve tasks when presented with unfamiliar materials (Herrmann et al., 2008, Mulcahy et al., 2012). Prior experience of tools and materials, as found in some non tool-using primates on similar Means-End tasks (Hauser et al., 2002b, Spaulding and Hauser, 2005), therefore appears to influence subjects' subsequent performances. Yet, no differences in the comprehension of object relationships were observed between macaws, which are highly neophobic of objects, and caiques, which are highly explorative of objects (Chapter 3). Although caiques have a greater interest, *per se*, in manipulating objects, their capacities to understand object relationships remain similar to those of macaws.

In a second novel Means-End task, the Trap-Gaps problem, macaws and caiques also showed comparable performances, although they required many trials before learning to solve their initial task. However, one caique spontaneously solved a novel transfer task, suggesting that it transferred relevant learned information from its previous experience of the initial task, across a functionally analogous, but novel, problem. One macaw also rapidly solved the transfer task, albeit not spontaneously (11 errors in 38 trials). These findings suggest that some caiques, and possibly some macaws, possess sophisticated capacities to generalise learned information across novel problems (Chapter 5) in this cognitive domain. Yet the spontaneous performance of one caique may also provide tentative evidence to suggest that caiques are more attentive to object relationships than macaws. However, with such limited sample sizes it remains difficult to support such conclusions without further testing. Future studies that incorporate larger numbers of subjects may therefore reveal more reliable conclusions.

7.1.3: Does Serial Reversal Learning Performance Correspond With Social Complexity?

Serial Reversal Learning has previously been considered as an index of behavioural flexibility, which may be particularly relevant to animals that require an ability to rapidly respond to complex social dynamics (Bond et al., 2007). Some of the most pronounced differences between macaws and caiques were revealed through detailed behavioural observations of their social interactions (Chapter 2). While the durations and frequencies of self-preening behaviours of macaws and caiques appear similar, caiques do not seem to preen others more than they preen themselves, whereas macaws preen others much more frequently than themselves. Consequently, macaws spend much more time than caiques engaging in affiliative behaviours (Chapter 2). Macaws were also observed in pairs more frequently than caiques, and spent more time in collective groups of four individuals than caiques (Chapter 2). By contrast, caiques were more frequently observed to engage in solitary behaviours, although they engaged in social play more frequently than macaws. When exploring objects, macaws generally approached items together as a group of four individuals (Chapter 3). Conversely, certain individual caiques (usually low ranking subordinates) were the first to interact with objects.

Overall findings suggest that macaws may be more social than caiques. Like other social, relatively large-brained species of birds, such as corvids, macaws may therefore be predicted to out-perform less social caiques on tasks that are associated with social complexity (Bond et al., 2003, 2007). Certainly there was some evidence, albeit a non-significant result due to a low sample size, that macaws learned an initial colour association and a subsequent reversal of these contingencies in fewer trials than caiques (Chapter 6). However, both macaws and caiques displayed similar Serial Reversal Learning performances, and also appeared to show capacities for flexible behaviours when trained to a particularly high learning criterion

(Chapter 6; 6.2). Macaws and caiques use highly reinforced associations to generate higher-order conditional rules to respond to alternating rewarded contingencies, rather than re-learning each reversal by lower-level processes of association and extinction. Irrespective of differences in the complexity of their social relationships, macaws and caiques appear to show comparable performances on Serial Reversal Learning tasks that have previously been linked to social complexity. The comparable, relatively large, brain-size of these subjects may therefore afford such behavioural flexibility.

7.2: Limitations of these experiments

One major constraint associated with this research, and other comparative studies, is the limited number of subjects used in each study. While it may be possible to identify some of the more fundamental characteristics of these two species when using a small sample size, subtle between-species differences may be lost due to within-species individual variation. A limited selection of subjects also relies on the compliance of certain individuals who are less motivated to participate in experiments. Individuals within each species often revealed dramatic variation in their performances and it was often difficult to acquire data from all subjects. Hence, with a much larger sample size, possibly 9-11 birds per group, these findings are likely to have been more robust and informative. Another constraint associated with a small sample size is the necessity to interpret all findings cautiously, as it is difficult to generalise the behaviours of only a few individuals to make broad species-wide comparisons, particularly between captive and wild species.

The above limitations, associated with small sample sizes, were however unavoidable. These studies were restricted to only four birds per species as a consequence of the available funding, the number of individuals that could be acquired from registered breeders, the space available for testing and the time required to individually test each bird. Parrots are also expensive animals to purchase and require much investment to maintain, both financially and socially.

In light of these limitations, similar studies, that use comparably small sample sizes, have reported striking findings (Bird and Emery, 2009a, Cheke et al., 2011, Seed et al., 2006). Parrots are however an excellent family to investigate physical and social cognition because they are highly social, inquisitive and enjoy the company of human experimenters.

7.3: Future Directions

Animal cognition is built on studies of socially isolated species in captivity. Although similar experiments to those presented in this thesis may be difficult to perform in the wild, such complementary research is likely to provide robust and ecologically valid results, and hence be valuable and much needed addition to advance the field of comparative cognition. Furthermore, many of the experiments reported here were undertaken while individuals were socially isolated. While this procedure is necessary to control for aspects of social learning, which may have biased results, these conditions are unlikely to be experienced by social species in the wild. Hence, experiments that assess cognitive behaviours of individuals within a more social setting, particularly those socially bonded species, may provide particularly valid ecological information.

Future studies may also benefit from testing pet parrots in a domestic setting. This approach has been successfully adopted for studies on dogs as it provides access to a wide variety of subjects of different breeds. Moreover, this approach avoids many of the problems associated with funding and maintaining large populations of subjects. However, testing domestic pet parrots involves an array of associated problems. I initially tried this approach and found it very difficult to extract unbiased data due to the inadvertent enthusiasm of proud pet owners.

Future studies may also provide valuable insight to cognitive evolution by comparing more closely related species, such as those within a given genus,

that have well established socio-ecological differences in their natural habitats, sociality or foraging behaviours. Hence, any divergences in cognitive behaviours may be directly inferred from differences in socio-ecological selection pressures, rather than common descent (Balda et al., 1996, Harvey and Pagel, 1991)

7.4: Concluding Remarks

The tendency to explore and interact with objects has been considered an adaptive trait that is driven by ecological selection pressures, such as the need to actively search for food in particular habitats, extract otherwise out of reach foods that are embedded in substrates, or manipulate foods encased in hard shells (Glickman and Sroges, 1966, Mettke-Hofmann et al., 2002, Webster and Lefebvre, 2000). The active manipulation of the environment, for example by using tools to extract otherwise inaccessible resources, may present further selection pressures that favour an understanding of the functional properties of tools, and causal reasoning that underlies certain behavioural actions (Byrne, 1997). Similarly, the ability to interpret and use social information has also been considered an important driver of cognitive evolution (Byrne and Whiten, 1988, Dunbar, 1998, Emery et al., 2007, Humphrey, 1976). For example, selection pressures may favour an ability to attend to social information, such as direction of attention conveyed through eye gaze or pointing to aid in the acquisition of resources (Dally et al., 2006, Emery et al., 1997, Hare et al., 2001). However, while cognition may have evolved in response to such domain specific problems, a by-product of cognitive evolution may result in the ability to adapt to domain general challenges. The two study species investigated here possess a similar relative brain size (Iwaniuk et al., 2005), thus suggesting similar levels of cognitive ability, and their contrasting natural habitats appear to coincide with divergent social and object-related behaviours. Indeed, both species appear to show equivalent performances on tasks associated with social and physical cognition. A relatively large brain size may therefore allow animals to respond

to a variety of socio-ecological challenges through behavioural flexibility (Emery and Clayton, 2004a, Sol et al., 2005).

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REFERENCES

- AIELLO, L. C. & WHEELER, P. (1995) The expensive-tissue hypothesis: the brain and the digestive system in human and primate evolution. *Current Anthropology*, 36, 199-221.
- AL AIN, S., GIRET, N., GRAND, M., KREUTZER, M. & BOVET, D. (2009) The discrimination of discrete and continuous amounts in African grey parrots (*Psittacus erithacus*). *Animal Cognition*, 12, 145-154.
- ALBIACH-SERRANO, A., T. B. & J. C. (2012) Apes (*Gorilla gorilla*, *Pan paniscus*, *P. troglodytes*, *Pongo abelii*) vs corvids (*Corvus corax*, *C. corone*) in a support task: The effect of pattern and functionality. *Journal of Comparative Psychology*, 126(4), 355-367.
- ALTMANN, J. (1974) Observational Study of Behaviour: Sampling Methods. *Behaviour*, 49, 227-267.
- AMICI, F., AURELI, F. & CALL, J. (2008) Fission-Fusion Dynamics, Behavioural Flexibility, and Inhibitory Control in Primates. *Current Biology*, 18, 1415-1419.
- ANDREWS, K. (2005) Chimpanzee theory of mind: Looking in all the wrong places? *Mind & Language*, 20, 521-536.
- AUERSPERG, A. M. I., GAJDON, G. K. & HUBER, L. (2009) Kea (*Nestor notabilis*) consider spatial relationships between objects in the support problem. *Biology Letters*, 5, 455-458.
- AUERSPERG, A. M. I., LAUMER, I. B. & BUGNYAR, T. (2013) Goffin cockatoos wait for qualitative and quantitative gains but prefer 'better' to 'more'. *Biology Letters*, 9, (in press).
- AUERSPERG, A. M. I., SZABO, B., VON BAYERN, A. M. P. & BUGNYAR, T. (in press) Object Permanence in the Goffin Cockatoo (*Cacatua goffini*). *Journal of Comparative Psychology*.
- AUERSPERG, A. M. I., SZABO, B., VON BAYERN, A. M. P. & KACELNIK, A. (2012) Spontaneous innovation in tool manufacture and use in a Goffin's cockatoo. *Current Biology*, 22, 903-904.
- AUERSPERG, A. M. I., VON BAYERN, A. M. P., GAJDON, G. K., HUBER, L. & KACELNIK, A. (2011) Flexibility in Problem Solving and Tool Use of Kea and New Caledonian Crows in a Multi Access Box Paradigm. *PLoS One*, 6, e20231.
- AURELI, F., SCHAFFNER, C. M., BOESCH, C., BEARDER, S. K., CALL, J., CHAPMAN, C. A., CONNOR, R., DI FIORE, A., DUNBAR, R. I. M., HENZI, S. P., HOLEKAMP, K., KORSTJENS, A. H., LAYTON, R., LEE, P., LEHMANN, J., MANSON, J. H., RAMOS-FERNANDEZ, G., STRIER, K. B. & VAN SCHAİK, C. P. (2008) Fission-Fusion Dynamics New Research Frameworks. *Current Anthropology*, 49, 627-654.
- BABB, S. J. & CRYSTAL, J. D. (2006a) Discrimination of what, when, and where is not based on time of day. *Learning & Behaviour*, 34, 124-130.
- BABB, S. J. & CRYSTAL, J. D. (2006b) Episodic-like memory in the rat. *Current Biology*, 16, 1317-1321.

- BAGOTSKAYA, M. S., SMIRNOVA, A. A. & ZORINA, Z. A. (2012) Corvidae Can Understand Logical Structure in Baited String-Pulling Tasks. *Neuroscience and Behavioural Physiology*, 42, 36-42.
- BALDA, R. P. & KAMIL, A. C. (1989) A comparative study of cache recovery by three corvid species. *Animal Behaviour*, 38, 486-495.
- BALDA, R. P. & KAMIL, A. C. (1992) Long-term spatial memory in Clark nutcracker (*Nucifraga columbiana*). *Animal Behaviour*, 44, 761-769.
- BALDA, R. P., KAMIL, A. C. & BEDNEKOFF, P. A. (1996) Predicting cognitive capacities from natural histories: Examples from four corvid species. *Current Ornithology*, 13, 33-66.
- BANG, A., DESHPANDE, S., SUMANA, A. & GADAGKAR, R. (2010) Choosing an appropriate index to construct dominance hierarchies in animal societies: a comparison of three indices. *Animal Behaviour*, 79, 631-636.
- BARNETT, S. A. (1958) Experiments on neophobia in wild and laboratory rats. *British Journal of Psychology*, 49, 195-201.
- BARTON, R. A. (1996) Neocortex size and behavioural ecology in primates. *Proceedings of the Royal Society of London Series B-Biological Sciences*, 263, 173-177.
- BARTON, R. A. (1998) Visual specialisation and brain evolution in primates. *Proceedings of the Royal Society of London Series B-Biological Sciences*, 265, 1933-1937.
- BEACH, F. A. (1950) The snark was a boojum. *American Psychologist*, 5, 115-124.
- BECK, B. B. (1980) *Animal Tool Behaviour*, Garland Press, New York.
- BEDNEKOFF, P. A. & BALDA, R. P. (1996a) Observational spatial memory in Clark's nutcrackers and Mexican jays. *Animal Behaviour*, 52, 833-839.
- BEDNEKOFF, P. A. & BALDA, R. P. (1996b) Social caching and observational spatial memory in pinyon jays. *Behaviour*, 133, 807-826.
- BEGGS, J. R. & WILSON, P. R. (1987) Energetics of South Island kaka (*Nestor meridionalis meridionalis*) feeding on the larvae of kanuka longhorn beetles (*Ochrocydus huttoni*). *New Zealand Journal of ecology*, 10, 143-147.
- BEKOFF, M. & BYERS, J. A. (1998) *Animal play: evolutionary, comparative and ecological perspectives*, Cambridge, Cambridge University Press.
- BENHAM, W. B. (1906) Notes on the flesh-eating propensity of the kea (*Nestor notabilis*). *Transactions of the Royal Society of New Zealand*, 39, 71-89.
- BENNETT, P. M. & HARVEY, P. H. (1985) Brain size, development and metabolism in birds and mammals. *Journal of Zoology*, 207, 491-509.
- BENSON-AMRAM, S. & HOLEKAMP, K. E. (2012) Innovative problem solving by wild spotted hyenas. *Proceedings of the Royal Society B: Biological Sciences*, 279, 4087-4095.
- BENSON-AMRAM, S., WELDELE, M. L. & HOLEKAMP, K. E. (2013) A comparison of innovative problem-solving abilities between wild and captive spotted hyenas, *Crocuta crocuta*. *Animal Behaviour*, 85, 349-356.
- BEREN, M. J., KLEIN, E. D., EVANS, T. A., CHAN, B., FLEMMING, T. M., HARRIS, E. H., WASHBURN, D. A. & RUMBAUGH, D. M. (2008) Discrimination Reversal Learning in Capuchin Monkeys (*Cebus apella*). *The Psychological Record*, 58, 3-14.

- BERTAGNOLIO, P. (1994) Tool-using by parrots: the palm cockatoo and the hyacinth macaw. *Avicultural Magazine*, 68-73.
- BIALYSTOK, E. & CODD, J. (2000) Representing quantity beyond whole numbers: Some, none, and part. *Canadian Journal of Experimental Psychology-Revue Canadienne De Psychologie Experimentale*, 54, 117-128.
- BIONDI, L. M., BO, M. S. & VASSALLO, A. I. (2010) Inter-individual and age differences in exploration, neophobia and problem-solving ability in a Neotropical raptor (*Milvago chimango*). *Animal Cognition*, 13, 701-710.
- BIRD, C. D. & EMERY, N. J. (2009a) Insightful problem solving and creative tool modification by captive nontool-using rooks. *Proceedings of the National Academy of Sciences of the United States of America*, 106, 10370-10375.
- BIRD, C. D. & EMERY, N. J. (2009b) Rooks use stones to raise the water level to reach a floating worm. *Current Biology*, 19, 1410-1414.
- BIRO, D., INOUE-NAKAMURA, N., TONOOKA, R., YAMAKOSHI, G., SOUSA, C. & MATSUZAWA, T. (2003) Cultural innovation and transmission of tool use in wild chimpanzees: Evidence from field experiments. *Animal Cognition*, 6, 213-223.
- BITTERMAN, M. E. (1960) Toward a comparative psychology of learning. *American Psychologist* 15, 704-712.
- BITTERMAN, M. E. (1965) Phyletic differences in learning. *American Psychologist*, 20, 396-410.
- BITTERMAN, M. E. (1975) Comparative analysis of learning - are laws of learning same in all animals. *Science*, 188, 699-709.
- BLUFF, L. A., WEIR, A. A. S., RUTZ, C., WIMPENNY, J. H. & KACELNIK, A. (2007) Tool-related cognition in New Caledonian crows. *Comparative Cognition & Behaviour Reviews*, 2, 1-25.
- BOEHRER, B. T. (2004) *Parrot Culture: Our 2500-year-long fascination with the world's most talkative bird.*, Philadelphia, University of Pennsylvania Press.
- BOESCH, C. (2007) What makes us human (*Homo sapiens*)? The challenge of cognitive cross-species comparison. *Journal of Comparative Psychology*, 121, 227-240.
- BOESCH, C. & BOESCH, H. (1990) Tool use and tool making in wild chimpanzees. *Folia Primatologica*, 54, 86-99.
- BOLHUIS, J. J. & MACPHAIL, E. M. (2001) A critique of the neuroecology of learning and memory. *Trends in Cognitive Sciences*, 5, 426-433.
- BOLIVAR, V. J. & FLAHERTY, L. (2004) Genetic control of novel food preference in mice. *Mammalian Genome* 15, 193-198.
- BOND, A. B., KAMIL, A. C. & BALDA, R. P. (2003) Social complexity and transitive inference in corvids. *Animal Behaviour*, 65, 479-487.
- BOND, A. B., KAMIL, A. C. & BALDA, R. P. (2007) Serial reversal learning and the evolution of behavioural flexibility in three species of North American corvids (*Gymnorhinus cyanocephalus*, *Nucifraga columbiana*, *Aphelocoma californica*). *Journal of Comparative Psychology*, 121, 372-379.
- BOOGERT, N. J., READER, S. M. & LALAND, K. N. (2006) The relation between social rank, neophobia and individual learning in starlings. *Animal Behaviour*, 72, 1229-1239.

- BORSARI, A. & OTTONI, E. B. (2005) Preliminary observations of tool use in captive hyacinth macaws (*Anodorhynchus hyacinthinus*). *Animal Cognition*, 8, 48-52.
- BOUCHARD, J., GOODYER, W. & LEFEBVRE, L. (2007) Social learning and innovation are positively correlated in pigeons (*Columba livia*). *Animal Cognition*, 10, 259-266.
- BOYSEN, S. T. & BERNTSON, G. G. (1989) Numerical competence in a chimpanzee (*Pan troglodytes*) *Journal of Comparative Psychology*, 103, 23-31.
- BRAUER, J., CALL, J. & TOMASELLO, M. (2005) All great ape species follow gaze to distant locations and around barriers. *Journal of Comparative Psychology*, 119, 145-154.
- BRELAND, K. & BRELAND, M. (1961) The misbehaviour of organisms. *American Psychologist*, 16, 681-684.
- BROUWER, K., JONES, M. L., KING, C. E. & SCHIFTER, H. (2000) Longevity records for Psittaciformes in captivity. *International Zoo Yearbook*, 37, 299-316.
- BUGNYAR, T. & HEINRICH, B. (2005) Ravens, *Corvus corax*, differentiate between knowledgeable and ignorant competitors. *Proceedings of the Royal Society B-Biological Sciences*, 272, 1641-1646.
- BUGNYAR, T. & KOTRSCHAL, K. (2002) Observational learning and the raiding of food caches in ravens (*Corvus corax*): Is it 'tactical' deception? *Animal Behaviour*, 64, 185-195.
- BUGNYAR, T., SCHWAB, C., SCHLOEGL, C., KOTRSCHAL, K. & HEINRICH, B. (2007) Ravens judge competitors through experience with play caching. *Current Biology*, 17, 1804-1808.
- BUGNYAR, T., STOWE, M. & HEINRICH, B. (2004) Ravens, *Corvus corax*, follow gaze direction of humans around obstacles. *Proceedings of the Royal Society of London Series B-Biological Sciences*, 271, 1331-1336.
- BURGER, J. & GOCHFELD, M. (2003) Parrot behaviour at a Rio Manu (Peru) clay lick: temporal patterns, associations, and antipredator responses. *Acta Ethologica*, 6, 23-34.
- BURISH, M. J., KUEH, H. Y. & WANG, S. S. H. (2004) Brain architecture and social complexity in modern and ancient birds. *Brain Behaviour and Evolution*, 63, 107-124.
- BYRNE, R. W. (1996) The misunderstood ape: cognitive skills of the gorilla. IN RUSSON, A. E., BARD, K. A. & PARKER, S. T. (Eds.) *Reaching into Thought: The Minds of the Great Apes*. Cambridge, UK, Cambridge University Press.
- BYRNE, R. W. (1997) The technical intelligence hypothesis: an additional evolutionary stimulus to intelligence? IN A. WHITEN & BYRNE, R. W. (Eds.) *Machiavellian intelligence II: extensions and evaluations*. Cambridge, UK, Cambridge University Press.
- BYRNE, R. W. (2004) The manual skills and cognition that lie behind hominid tool use. IN RUSSON, A. E. & BEGUN, D. R. (Eds.) *The Evolution of Thought: Evolutionary Origins of Great Ape Intelligence*. Cambridge, UK, Cambridge University Press.
- BYRNE, R. W. & BATES, L. A. (2009) Elephant cognition in primate perspective. *Comparative Cognition Reviews*, 65-79.

- BYRNE, R. W. & CORP, N. (2004) Neocortex size predicts deception rate in primates. *Proceedings of the Royal Society of London Series B-Biological Sciences*, 271, 1693-1699.
- BYRNE, R. W. & WHITEN, A. (1985) Tactical deception of familiar individuals in baboons (*Papio ursinus*). *Animal Behaviour*, 33, 669-673.
- BYRNE, R. W. & WHITEN, A. (1988) *Machiavellian intelligence: social expertise and the evolution of intellect in monkeys, apes, and humans*, Oxford, Clarendon Press.
- CALL, J. (2004) Inferences about the location of food in the great apes (*Pan paniscus*, *Pan troglodytes*, *Gorilla gorilla*, and *Pongo pygmaeus*). *Journal of Comparative Psychology*, 118, 232-241.
- CALL, J., AGNETTA, B. & TOMASELLO, M. (2000) Social cues that chimpanzees do and do not use to find hidden objects. *Animal Cognition*, 3, 23-34.
- CALL, J., HARE, B. & TOMASELLO, M. (1998) Chimpanzee gaze following in an object-choice task. *Animal Cognition*, 89-99.
- CARTER, P. (2006) *Parrot*, London, Reaktion Books.
- CHAPPELL, J. & KACELNIK, A. (2002) Tool selectivity in a non-primate, the New Caledonian crow (*Corvus moneduloides*). *Animal Cognition*, 5, 71-78.
- CHAPPELL, J. & KACELNIK, A. (2004) Selection of tool diameter by New Caledonian crows (*Corvus moneduloides*). *Animal Cognition*, 7, 121-127.
- CHEKE, L., BIRD, C. & CLAYTON, N. (2011) Tool-use and instrumental learning in the Eurasian jay (*Garrulus glandarius*). *Animal Cognition*, 1-15.
- CHIARATI, E., CANESTRARI, D., VERA, R. & BAGLIONE, V. (2012) Subordinates benefit from exploratory dominants: response to novel food in cooperatively breeding carrion crows. *Animal Behaviour*, 83, 103-109.
- CHITTKA, L. & NIVEN, J. (2009) Are bigger brains better? *Current Biology*, 19, 995-1008.
- CLARK, C. M. H. (1970) Observations on population, movements and food of the kea (*Nestor notabilis*). *Notornis*, 17, 105-114.
- CLARKE, A. S. & LINDBURG, D. G. (1993) Behavioural contrasts between male cynomolgus and lion-tailed macaques. *American Journal of Primatology*, 29, 49-59.
- CLAYTON, N. S., BUSSEY, T. J. & DICKINSON, A. (2003a) Can animals recall the past and plan for the future? . *Nature Reviews Neuroscience*, 4, 685-691.
- CLAYTON, N. S., CORREIA, S. P. C., RABY, C. R., ALEXIS, D. M., EMERY, N. J. & DICKINSON, A. (2008) Response to Suddendorf & Corballis (2008): in defence of animal foresight. *Animal Behaviour*, 76, E9-E11.
- CLAYTON, N. S., DALLY, J. M. & EMERY, N. J. (2007) Social cognition by food-caching corvids: The Western scrub-jay as a natural psychologist. *Philosophical Transactions of the Royal Society B-Biological Sciences*, 362, 507-522.
- CLAYTON, N. S. & DICKINSON, A. (1998) Episodic-like memory during cache recovery by scrub jays. *Nature*, 395, 272-274.
- CLAYTON, N. S. & DICKINSON, A. (1999) Scrub jays (*Aphelocoma coerulescens*) remember the relative time of caching as well as the location and content of their caches. *Journal of Comparative Psychology*, 113, 403-416.

- CLAYTON, N. S., GRIFFITHS, D. P. & BENNETT, A. D. (1996) Storage of stones by jays (*Garrulus glandarius*). *Ibis*, 136, 331–34.
- CLAYTON, N. S. & RUSSELL, J. (2009) Looking for episodic memory in animals and young children: Prospects for a new minimalism. *Neuropsychologia*, 47, 2330-2340.
- CLAYTON, N. S., RUSSELL, J. & DICKINSON, A. (2009) Are Animals Stuck in Time or Are They Chronesthetic Creatures? *Topics in Cognitive Science*, 1, 59-71.
- CLAYTON, N. S., YU, K. S. & DICKINSON, A. (2001) Scrub jays (*Aphelocoma coerulescens*) form integrated memories of the multiple features of caching episodes. *Journal of Experimental Psychology-Animal Behaviour Processes*, 27, 17-29.
- CLAYTON, N. S., YU, K. S. & DICKINSON, A. (2003b) Interacting cache memories: Evidence for flexible memory use by Western scrub-Jays (*Aphelocoma californica*). *Journal of Experimental Psychology-Animal Behaviour Processes*, 29, 14-22.
- CLUTTON-BROCK, T. H. & HARVEY, P. H. (1980) Primates, brains and ecology. *Journal of Zoology, London*, 190, 309-323.
- COCKBURN, A. (1991) *An introduction to evolutionary ecology*, Blackwell.
- COLE, E., MORAND-FERRON, J., HINKS, A. & QUINN, J. (2012) Cognitive Ability Influences Reproductive Life History Variation in the Wild. *Current Biology*, 22, 1808-1812.
- COLE, E. & QUINN, J. (2012) Personality and problem-solving performance explain competitive ability in the wild. *Proceedings of the Royal Society Biological Sciences*, 22, 1168–1175.
- COLE, E. F., CRAM, D. L. & QUINN, J. L. (2011) Individual variation in spontaneous problem-solving performance among wild great tits. *Animal Behaviour*, 81, 491-498.
- COLEMAN, S. L. & MELLGREN, R. L. (1994) Neophobia when feeding alone or in flocks in zebra finches, *Taeniopygia guttata*. *Animal Behaviour*, 48, 903-907.
- CONNOR, R. C. (2007) Dolphin social intelligence: complex alliance relationships in bottlenose dolphins and a consideration of selective environments for extreme brain size evolution in mammals. *Philosophical Transactions of the Royal Society B-Biological Sciences*, 362, 587-602.
- CONNOR, R. C., MANN, J., TYACK, P. L. & WHITEHEAD, H. (1998) Social evolution in toothed whales. *Trends in Ecology & Evolution*, 13, 228-232.
- CONNOR, R. C., SMOLKER, R. A. & RICHARDS, A. F. (1992) Dolphin alliances and coalitions. IN HARCOURT, A. H. & WAAL, F. B. M. D. (Eds.) *Coalitions and Alliances in Humans and Other Animals*. Oxford, UK, Oxford University Press.
- COREY, D. T. (1978) The determinants of exploration and neophobia. *Neuroscience and Biobehavioural Reviews*, 2, 235-53.
- CORREIA, S. P. C., DICKINSON, A. & CLAYTON, N. S. (2007) Western scrub-jays anticipate future needs independently of their current motivational state. *Current Biology*, 17, 856-861.
- CRAMP, S. & PERRINS, C. (1994) The birds of the Western Palearctic. Crows to finches. *Handbook of the birds of Europe, the Middle East and North Africa*. Oxford, UK, Oxford University Press.

- CRISTOL, D. A. & SWITZER, P. V. (1999) Avian prey-dropping behaviour. II. American crows and walnuts. *Behavioural Ecology*, 10, 220-226.
- CUNNINGHAM, C. L., ANDERSON, J. R. & MOOTNICK, A. R. (2006) Object manipulation to obtain a food reward in hoolock gibbons, *Bunopithecus hoolock*. *Animal Behaviour*, 71, 621–629.
- CUTHBERT, R. (2003) Sign left by introduced and native predators feeding on Hutton's shearwaters (*Puffinus huttoni*). *New Zealand Journal of Zoology*, 30, 163-170.
- DALLY, J. M., EMERY, N. J. & CLAYTON, N. S. (2004) Cache protection strategies by Western scrub-jays (*Aphelocoma californica*): hiding food in the shade. *Proc Biol Sci*, 271 Suppl 6, S387-90.
- DALLY, J. M., EMERY, N. J. & CLAYTON, N. S. (2005) Cache protection strategies by Western scrub-jays (*Aphelocoma californica*): implications for social cognition. *Animal Behaviour*, 70, 1251-1263.
- DALLY, J. M., EMERY, N. J. & CLAYTON, N. S. (2006) Food-caching Western scrub-jays keep track of who was watching when. *Science*, 312, 1662-1665.
- DARWIN, C. (1859) *The origin of species* London, John Murray.
- DARWIN, C. (1897) *The decent of man and selection in relation to sex (rev. edn.)*, New York, Appleton (originally published 1871)
- DAVID, H. A. (1987) Ranking from unbalanced paired-comparison data. *Biometrika*, 74, 432-436.
- DAY, L. B., CREWS, D. & WILCZYNSKI, W. (1999) Spatial and reversal learning in congeneric lizards with different foraging strategies. *Animal Behaviour*, 57, 393-407.
- DAY, R. L., COE, R. L., KENDAL, J. R. & LALAND, K. N. (2003) Neophilia, innovation and social learning: a study of intergeneric differences in callitrichid monkeys. *Animal Behaviour*, 65, 559-571.
- DE KORT, S. R., DICKINSON, A. & CLAYTON, N. S. (2005) Retrospective cognition by food-caching western scrub-jays. *Learning and Motivation*, 36, 159-176.
- DE KORT, S. R., EMERY, N. J. & CLAYTON, N. S. (2003) Food offering in jackdaws (*Corvus monedula*). *Naturwissenschaften*, 90, 238-240.
- DE KORT, S. R., EMERY, N. J. & CLAYTON, N. S. (2006) Food sharing in jackdaws, *Corvus monedula*: what, why and with whom? *Animal Behaviour*, 72, 297-304.
- DE LILLO, C. & VISALBERGHI, E. (1994) Transfer index and mediational learning in tufted capuchins (*Cebus apella*). *International Journal of Primatology*, 15, 275-287.
- DE MENDONCA-FURTADO, O. & OTTONI, E. B. (2008) Learning generalisation in problem solving by a blue-fronted parrot (*Amazona aestiva*). *Animal Cognition*, 11, 719-725.
- DE VRIES, H., STEVENS, J. M. G. & VERVAECKE, H. (2006) Measuring and testing the steepness of dominance hierarchies. *Animal Behaviour*, 71, 585-592.
- DE WAAL, F. (1982) *Chimpanzee Politics*, London, Jonathan Cape.

- DE WAAL, F. B. M. & LUTRELL, L. M. (1988) Mechanisms of social reciprocity in three primate species: symmetrical relationship characteristics or cognition? *Ethology and Sociobiology*, 101–118.
- DE WAAL, F. B. M. & TYACK, P. L. (2003) *Animal social complexity*, Cambridge, MA, Harvard University Press.
- DEANER, R. O., ISLER, K., BURKART, J. & VAN SCHAİK, C. P. (2007) Overall brain size, and not encephalization quotient, best predicts cognitive ability across non-human primates. *Brain Behaviour and Evolution*, 115-124.
- DEMERY, Z. P., CHAPPELL, J. & MARTIN, G. R. (2011) Vision, touch and object manipulation in Senegal parrots *Poicephalus senegalus*. *Proceedings of the Royal Society B: Biological Sciences*, 278, 3687-3693.
- DIAMOND, J. & BOND, A. B. (1999) *Kea, Bird of Paradox: the evolution and behaviour of a New Zealand parrot*, University of California Press, Berkeley, Los Angeles, London.
- DIAMOND, J. & BOND, A. B. (2003) A comparative analysis of social play in birds. *Behaviour*, 140, 1091-1115.
- DIAMOND, J., EASON, D., REID, C. & BOND, A. B. (2006) Social play in kakapo (*Strigops habroptilus*) with comparisons to kea (*Nestor notabilis*) and kaka (*Nestor meridionalis*). *Behaviour*, 143, 1397-1423.
- DINGEMANSE, N. J., BOTH, C., DRENT, P. J., VAN OERS, K. & VAN NOORDWIJK, A. J. (2002) Repeatability and heritability of exploratory behaviour in great tits from the wild. *Animal Behaviour*, 64, 929-938.
- DRENT, P. J., OERS, K. V. & NOORDWIJK, A. J. V. (2003) Realised heritability of personalities in the great tit (*Parus major*). *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 270, 45-51.
- DUCKER, G. & RENSCH, B. (1977) Solution of patterned string problems by birds. *Behaviour*, 62, 164-173.
- DUNBAR, R. I. M. (1992) Neocortex size as a constraint on group-size in primates. *Journal of Human Evolution*, 22, 469-493.
- DUNBAR, R. I. M. (1995) Neocortex size and group-size in primates - a test of the hypothesis. *Journal of Human Evolution*, 28, 287-296.
- DUNBAR, R. I. M. (1998) The social brain hypothesis. *Evolutionary Anthropology*, 6, 178-190.
- DUNBAR, R. I. M. & SHULTZ, S. (2007) Evolution in the social brain. *Science*, 317, 1344-1347.
- DURLACH, P. J. & MACKINTOSH, N. J. (1986) Transfer of serial reversal learning in the pigeon. *The Quarterly Journal of Experimental Psychology Section B*, 38, 81-95.
- ECHEVERRIA, A. I., VASSALLO, A. I. & ISACCH, J. P. (2006) Experimental analysis of novelty responses in a bird assemblage inhabiting a suburban marsh. *Canadian Journal of Zoology*, 84, 974-980.
- EMERY, N. J. (2000) The eyes have it: the neuroethology, function and evolution of social gaze. *Neuroscience and Biobehavioural Reviews*, 24, 581-604.
- EMERY, N. J. (2004) Are corvids 'feathered apes'? Cognitive evolution in crows, jays, rooks and jackdaws. IN WATANABE, S. (Ed.) *Comparative analysis of minds* Tokyo, Japan, Keio University Press.

- EMERY, N. J. (2006) Cognitive ornithology: the evolution of avian intelligence. *Philosophical Transactions of the Royal Society B-Biological Sciences*, 361, 23-43.
- EMERY, N. J. & CLAYTON, N. S. (2001) Effects of experience and social context on prospective caching strategies by scrub jays. *Nature*, 414, 443-446.
- EMERY, N. J. & CLAYTON, N. S. (2004b) The mentality of crows: convergent evolution of intelligence in corvids and apes. *Science*, 306, 1903-1907.
- EMERY, N. J. & CLAYTON, N. S. (2004a) Comparing the complex cognition of birds and primates IN ROGERS, L. J. & KAPLAN, G. (Eds.) *Comparative vertebrate cognition: are primates superior to nonprimates?* New York, Kluwer Academic Press.
- EMERY, N. J. & CLAYTON, N. S. (2005) Evolution of the avian brain and intelligence. *Current Biology*, 15, R946-R950.
- EMERY, N. J. & CLAYTON, N. S. (2008) How to build a scrub-jay that reads minds. IN ITAKURA, S. & FUJITA, K. (Eds.) *Origins of the Social Mind: Evolutionary & developmental views*.
- EMERY, N. J. & CLAYTON, N. S. (2009a) Comparative social cognition. *Annual Review of Psychology*, 60, 87-113.
- EMERY, N. J. & CLAYTON, N. S. (2009b) Tool use and physical cognition in birds and mammals. *Current Opinion in Neurobiology*, 19, 27-33.
- EMERY, N. J., LORINCZ, E. N., PERRETT, D. I., ORAM, M. W. & BAKER, C. I. (1997) Gaze following and joint attention in rhesus monkeys (*Macaca mulatta*). *Journal of Comparative Psychology*, 111, 286-293.
- EMERY, N. J., SEED, A. M., VON BAYERN, A. M. P. & CLAYTON, N. S. (2007) Cognitive adaptations of social bonding in birds. *Philosophical Transactions of the Royal Society B-Biological Sciences*, 362, 489-505.
- ENGH, A. L., SIEBERT, E. R., GREENBERG, D. A. & HOLEKAMP, K. E. (2005) Patterns of alliance formation and postconflict aggression indicate spotted hyaenas recognise third-party relationships. *Animal Behaviour*, 69, 209-217.
- ESSOCK-VITALE, S. M. (1978) Comparison of ape and monkey modes of problem solution. *Journal of Comparative and Physiological Psychology*, 92, 942-957.
- FAGEN, R. (1981) *Animal play behaviour*, New York, Oxford University Press.
- FEENEY, M. C., ROBERTS, W. A. & SHERRY, D. F. (2009) Memory for what, where, and when in the black-capped chickadee (*Poecile atricapillus*). *Animal Cognition*, 12, 767-777.
- FELSENSTEIN, J. (1985) Phylogenies and the comparative method. *American Naturalist*, 125, 1-15.
- FITCH, W. T., HUBER, L. & BUGNYAR, T. (2010) Social Cognition and the Evolution of Language: Constructing Cognitive Phylogenies. *Neuron*, 65, 795-814.
- FORSHAW, J. M. (1989) *Parrots of the world*, London, Blandford.
- FOX, R. A. & MILLAM, J. R. (2004) The effect of early environment on neophobia in orange-winged Amazon parrots (*Amazona amazonica*). *Applied Animal Behaviour Science*, 89, 117-129.

- FOX, R. A. & MILLAM, J. R. (2007) Novelty and individual differences influence neophobia in orange-winged Amazon parrots (*Amazona amazonica*). *Applied Animal Behaviour Science*, 104, 107-115.
- FRAGASZY, D., IZAR, P., VISALBERGHI, E., OTTONI, E. B. & DE OLIVEIRA, M. G. (2004) Wild capuchin monkeys (*Cebus libidinosus*) use anvils and stone pounding tools. *American Journal of Primatology*, 64, 359-366.
- FRAGASZY, D., PICKERING, T., LIU, Q., IZAR, P., OTTONI, E. & VISALBERGHI, E. (2010) Bearded capuchin monkeys' and a human's efficiency at cracking palm nuts with stone tools: Field experiments. *Animal Behaviour*, 79, 321-332.
- FUJITA, K., KUROSHIMA, H. & ASAI, S. (2003) How do tufted capuchin monkeys (*Cebus apella*) understand causality involved in tool use? *Journal of Experimental Psychology: Animal Behaviour Processes*, 29, 233-242
- FUNK, M. S. (1996a) Development of object permanence in the New Zealand parakeet (*Cyanoramphus auriceps*). *Animal Learning & Behaviour*, 24, 375-383.
- FUNK, M. S. (1996b) Spatial skill development in golden-crowned parakeets (*Cyanoramphus auriceps*): A Piagetian assessment. *Bird Behaviour*, 11, 91-104.
- FUNK, M. S. (2002) Problem solving skills in young yellow-crowned parakeets (*Cyanoramphus auriceps*). *Animal Cognition*, 5, 167-176.
- GAJDON, G. K., FIJN, N. & HUBER, L. (2004) Testing social learning in a wild mountain parrot, the kea (*Nestor notabilis*). *Learning & Behaviour*, 32, 62-71.
- GAJDON, G. K., FIJN, N. & HUBER, L. (2006) Limited spread of innovation in a wild parrot, the kea (*Nestor notabilis*). *Animal Cognition*, 9, 173-181.
- GALETTI, M. & RODRIGUES, M. (1992) Comparative Seed Predation on Pods by Parrots in Brazil. *Biotropica*, 24, 222-224.
- GAMMELL, M. P., DE VRIES, H., JENNINGS, D. J., CARLIN, C. M. & HAYDEN, T. J. (2003) David's score: a more appropriate dominance ranking method than Clutton-Brock et al.'s index. *Animal Behaviour*, 66, 601-605.
- GARAMSZEGI, L. Z., MOLLER, A. P. & ERRITZOE, J. (2002) Coevolving avian eye size and brain size in relation to prey capture and nocturnality. *Proceedings of the Royal Society Biological Sciences*, 961-967.
- GENTNER, T. Q., FENN, K. M., MARGOLIASH, D. & NUSBAUM, H. C. (2006) Recursive syntactic pattern learning by songbirds. *Nature*, 440, 1204-1207.
- GIBSON, K. R. (1986) Cognition, brain size and the extraction of embedded food resources. IN ELSE, J. G. & LEE, P. C. (Eds.) *Primate Ontogeny, Cognition and Social Behaviour* Cambridge, UK, Cambridge University Press.
- GILARDI, J. D. & MUNN, C. A. (1998) Patterns of Activity, Flocking, and Habitat Use in Parrots of the Peruvian Amazon. *The Condor*, 100, 641-653.
- GIRET, N., MIKLOSI, A., KREUTZER, M. & BOVET, D. (2009a) Use of experimenter-given cues by African gray parrots (*Psittacus erithacus*). *Animal Cognition*, 12, 1-10.
- GIRET, N., MONBUREAU, M., KREUTZER, M. & BOVET, D. (2009b) Conspecific discrimination in an object-choice task in African grey parrots (*Psittacus erithacus*). *Behavioural Processes*, 82, 75-77.

- GIRET, N., PERON, F., NAGLE, L., KREUTZER, M. & BOVET, D. (2009c) Spontaneous categorisation of vocal imitations in African grey parrots (*Psittacus erithacus*). *Behavioural Processes*, 82, 244-248.
- GIRNDT, A., MEIER, T. & CALL, J. J. (2008) Task constraints mask great apes' ability to solve the Trap-Table task. *Journal of Experimental Psychology: Animal Behaviour Processes*, 54-62.
- GLICKMAN, S. E. & SROGES, R. W. (1966) Curiosity in Zoo Animals. *Behaviour*, 26, 151-188.
- GODFREY-SMITH, P. (2002) Environmental complexity and the evolution of cognition. IN STERNBERG, R. & KAUFMAN, J. (Eds.) *The evolution of intelligence*. London, UK, Lawrence Erlbaum Associates.
- GONZALEZ, R. C., BERGER, B. D. & BITTERMAN, M. E. (1966) Improvement in habit-reversal as a function of the amount of training per reversal and other variables. *American Journal of Psychology*, 517-524.
- GOODALL, J. (1963) Feeding behaviour of wild chimpanzees: a preliminary report. *Symposium of the Zoological Society of London*, 39-48.
- GOODALL, J. (1986) *The Chimpanzees of Gombe: Patterns of Behaviour*, Cambridge, Mass., USA, Harvard University Press.
- GOSSETTE, R. L. (1969) Magnitude of negative transfer by myna birds on a spatial SDR task as a function of stringency of reversal criterion. *Perceptual and Motor Skills*, 29, 621-622.
- GOSSETTE, R. L., GOSSETTE, M. F. & RIDDELL, W. (1966) Comparisons of successive discrimination reversal performances among closely and remotely related avian species. *Animal Behaviour*, 14, 560-564.
- GOULD, S. J. (1997) The exaptive excellence of spandrels as a term and prototype. *Proceedings of the National Academy of Sciences of the United States of America*, 94, 10750-10755.
- GOULD, S. J. & LEWONTIN, R. C. (1979) Spandrels of San-Marco and the Panglossian paradigm: a critique of the adaptationist program. *Proceedings of the Royal Society of London Series B-Biological Sciences*, 205, 581-598.
- GREENBERG, R. (1983) The role of neophobia in determining the degree of foraging specialisation in some migrant warblers. *American Naturalist*, 122, 444-453.
- GREENBERG, R. (1984) Differences in feeding neophobia in the tropical migrant wood warblers *Dendroica castanea* and *D. pensylvanica*. *Journal of Comparative Psychology*, 98, 131-136.
- GREENBERG, R. (1990) Feeding neophobia and ecological plasticity - A test of the hypothesis with captive sparrows. *Animal Behaviour*, 39, 375-379.
- GREENBERG, R. (1992) Differences in Neophobia between Naive Song and Swamp Sparrows. *Ethology*, 91, 17-24.
- GREENBERG, R. (2003) The role of neophobia and neophilia in the development of innovative behaviour of birds IN S. M. READER & LALAND, K. N. (Eds.) *Animal Innovation*. New York, Oxford University Press.
- GREENBERG, R. & METTKE-HOFMANN N, C. (2001) Ecological aspects of neophobia and neophilia in birds. IN NOLAN, V., JR. & THOMPSON, C. F. (Eds.) *Current Ornithology*. Plenum Publishing Corporation.

- GRODZINSKI, U. & CLAYTON, N. S. (2010) Problems faced by food-caching corvids and the evolution of cognitive solutions. *Philosophical Transactions of the Royal Society B-Biological Sciences*, 365, 977-987.
- HAIN, J. H. W., CARTER, G. R., KRAUS, S. D., MAYO, C. A. & WINN, H. E. (1982) Feeding behaviour of the humpback whale, *Megaptera novaeangliae*, in the Western North-Atlantic. *Fishery Bulletin*, 80, 259-268.
- HANUS, D. & CALL, J. (2007) Discrete quantity judgments in the great apes (*Pan paniscus*, *Pan troglodytes*, *Gorilla gorilla*, *Pongo pygmaeus*): The effect of presenting whole sets versus item-by-item. *Journal of Comparative Psychology*, 121, 241-249.
- HANUS, D., MENDES, N., TENNIE, C. & CALL, J. (2011) Comparing the Performances of Apes (*Gorilla gorilla*, *Pan troglodytes*, *Pongo pygmaeus*) and Human Children (*Homo sapiens*) in the Floating Peanut Task. *PLoS One*, 6, e19555.
- HARE, B., BROWN, M., WILLIAMSON, C. & TOMASELLO, M. (2002) The domestication of social cognition in dogs. *Science*, 298, 1634-1636.
- HARE, B., CALL, J., AGNETTA, B. & TOMASELLO, M. (2000) Chimpanzees know what conspecifics do and do not see. *Animal Behaviour*, 59, 771-785.
- HARE, B., CALL, J. & TOMASELLO, M. (2001) Do chimpanzees know what conspecifics know? *Animal Behaviour*, 61, 139-151.
- HARE, B. & TOMASELLO, M. (2005) Human-like social skills in dogs? *Trends in Cognitive Sciences*, 9, 439-444.
- HARVEY, P. H., CLUTTONBROCK, T. H. & MACE, G. M. (1980) Brain size and ecology in small mammals and primates. *Proceedings of the National Academy of Sciences of the United States of America-Biological Sciences*, 77, 4387-4389.
- HARVEY, P. H. & PAGEL, M. D. (1991) *The comparative method in evolutionary biology* Oxford, Oxford University Press.
- HAUSER, M. D. (1997) Artfactual kinds and functional design features: what a primate understands without language. *Cognition*, 64, 285-308.
- HAUSER, M. D., CHOMSKY, N. & FITCH, W. T. (2002a) The Faculty of Language: What Is It, Who Has It, and How Did It Evolve? *Science*, 298, 1569-1579.
- HAUSER, M. D., KRALIK, J. & BOTTO-MAHAN, C. (1999) Problem solving and functional design features: experiments on cotton-top tamarins, *Saguinus oedipus oedipus*. *Animal Behaviour*, 57, 565-582.
- HAUSER, M. D., SANTOS, L. R., SPAEPEN, G. M. & PEARSON, H. E. (2002b) Problem solving, inhibition and domain-specific experience: experiments on cottontop tamarins, *Saguinus oedipus*. *Animal Behaviour*, 64, 387-396.
- HEALY, S. D., BACON, I. E., HAGGIS, O., HARRIS, A. P. & KELLEY, L. A. (2009) Explanations for variation in cognitive ability: Behavioural ecology meets comparative cognition. *Behavioural Processes*, 80, 288-294.
- HEALY, S. D. & ROWE, C. (2007) A critique of comparative studies of brain size. *Proceedings of the Royal Society B-Biological Sciences*, 274, 453-464.
- HEINRICH, B. (1988) Why Do Ravens Fear Their Food? *The Condor*, 90, 950-952.
- HEINRICH, B. (1995a) An Experimental Investigation of Insight in Common Ravens (*Corvus corax*). *The Auk*, 112, 994-1003.

- HEINRICH, B. (1995b) Neophilia and exploration in juvenile common ravens, *Corvus corax*. *Animal Behaviour*, 50, 695-704.
- HEINRICH, B. (1999) *Mind of the Raven*, New York, Harper Collins Publishers.
- HEINRICH, B. & BUGNYAR, T. (2005) Testing problem solving in ravens: string-pulling to reach food. *Ethology*, 111, 962-976.
- HEINRICH, B., MARZLUFF, J. & ADAMS, W. (1995) Fear and Food Recognition in Naive Common Ravens. *The Auk*, 112, 499-503.
- HERRMANN, E., HARE, B., CALL, J. & TOMASELLO, M. (2010) Differences in the cognitive skills of bonobos and chimpanzees. *PLoS One*, 5, e12438.
- HERRMANN, E., WOBBER, V. & CALL, J. (2008) Great apes' (*Pan troglodytes*, *Pan paniscus*, *Gorilla gorilla*, *Pongo pygmaeus*) understanding of tool functional properties after limited experience. *Journal of Comparative Psychology*, 122, 220-230.
- HEYES, C. (2003) Four routes of cognitive evolution. *Psychological Review*, 110, 713-727.
- HEYES, C. & SAGGERSON, A. (2002) Testing for imitative and nonimitative social learning in the budgerigar using a two-object/two-action test. *Animal Behaviour*, 64, 851-859.
- HIHARA, S., OBAYASHI, S., TANAKA, M. & IRIKI, A. (2003) Rapid learning of sequential tool use by macaque monkeys. *Physiology & Behaviour*.
- HODOS, W. (1993) The Visual Capabilities of Birds. IN ZEIGLER & BISCHOF (Eds.) *Vision, brain, and behaviour in birds*. Cambridge, MA, MIT Press.
- HODOS, W. & CAMPBELL, C. B. G. (1969) Scala naturae: Why there is no theory in comparative psychology. *Psychological Review*, 76, 337-350.
- HOHMANN, G. & FRUTH, B. (2008) New records on prey capture and meat eating by bonobos at Lui Kotale, Salonga National Park, Democratic Republic of Congo. *Folia Primatologica*, 79, 103-110.
- HOLEKAMP, K. E., SAKAI, S. T. & LUNDRIGAN, B. L. (2007) Social intelligence in the spotted hyena (*Crocuta crocuta*). *Philosophical Transactions of the Royal Society B*, 362, 523-538.
- HUBER, L. & GAJDON, G. K. (2006) Technical intelligence in animals: the kea model. *Animal Cognition*, 9, 295-305.
- HUBER, L., RECHBERGER, S. & TABORSKY, M. (2001) Social learning affects object exploration and manipulation in keas, *Nestor notabilis*. *Animal Behaviour*, 62, 945-954.
- HULL, C. L. (1943) *Principles of behaviour*, New York, NY, Appleton- Century-Crofts.
- HUMPHREY, N. K. (1976) The social function of intellect IN BATESON, P. P. G. & HINDE, R. A. (Eds.) *Growing Points in Ethology*. Cambridge, Cambridge University Press.
- HUNT, G. R. (1996) Manufacture and use of hook-tools by New Caledonian crows. *Nature*, 379, 249-251.
- HUNT, G. R., CORBALLIS, M. C. & GRAY, R. D. (2006) Design complexity and strength of laterality are correlated in New Caledonian crows' Pandanus tool manufacture. *Proceedings of the Royal Society B*, 273, 1127-1133.

- HUNT, G. R. & GRAY, R. D. (2003) Diversification and cumulative evolution in New Caledonian crow tool manufacture. *Proceedings of the Royal Society of London Series B-Biological Sciences*, 270, 867-874.
- HUNT, G. R. & GRAY, R. D. (2004) The crafting of hook tools by wild New Caledonian crows. *Proceedings of the Royal Society B: Biology Letters*, 271, S88–S90.
- HUNT, S., LOW, J. & BURNS, K. C. (2008) Adaptive numerical competency in a food-hoarding songbird. *Proceedings of the Royal Society B-Biological Sciences*, 275, 2373-2379.
- HUNTER, M. W. & KAMIL, A. C. (1971) Object discrimination learning set and hypothesis behaviour in the northern bluejay (*Cynaocitta cristata*). *Psychonomic Science*, 22, 271–273.
- HUSBAND, S. & SHIMIZU, T. (2001) Evolution of the avian visual system. IN COOG, R. G. (Ed.) *Avian Visual Cognition*. Available on-line: www.pigeon.psy.tufts.edu/avc/shimp.
- IRIE-SUGIMOTO, N., KOBAYASHI, T., SATO, T. & HASEGAWA, T. (2008) Evidence of means-end behaviour in Asian elephants (*Elephas maximus*). *Animal Cognition*, 11, 359-365.
- ISLER, K. & VAN SCHAIK, C. P. (2009) Why are there so few smart mammals (but so many smart birds)? *Biology Letters* 125-129.
- IWANIUK, A. N., DEAN, K. M. & NELSON, J. E. (2003) The evolution of parrot brains: comparisons with primates and other birds. *Society for Neuroscience Abstract Viewer and Itinerary Planner*, 2003, Abstract No. 94.8.
- IWANIUK, A. N., DEAN, K. M. & NELSON, J. E. (2005) Interspecific allometry of the brain and brain regions in parrots (*psittaciformes*): comparisons with other birds and primates. *Brain Behaviour and Evolution*, 65, 40-59.
- IWANIUK, A. N. & NELSON, J. E. (2003) Developmental differences are correlated with relative brain size in birds: a comparative analysis. *Canadian Journal of Zoology-Revue Canadienne De Zoologie*, 81, 1913-1928.
- IWANIUK, A. N., NELSON, J. E. & PELLIS, S. M. (2001) Do big-brained animals play more? Comparative analysis of play and relative brain size in mammals. *Journal of Comparative Psychology*, 115, 29-41.
- JANMAAT, K. R. L., BYRNE, R. W. & ZUBERBUHLER, K. (2006) Evidence for a spatial memory of fruiting states of rainforest trees in wild mangabeys. *Animal Behaviour*, 797-807.
- Jarvis, E. D., Gunturkun, O., Bruce, L., Csillag, A., Karten, H., Kuenzel, W., Medina, L., Paxinos, G., Perkel, D. J., Shimizu, T., Striedter, G., Wild J. M., Ball, G. F., Dugas-Ford, J., Durand, S. E., Hough, G. E., Husband, S., Kubikova, L., Lee, D. W., Mello, C. V., Powers, A., Siang, C., Smulders, T. V., Wada, K., White, S. A., Yamamoto, K., Yu, J., Reiner, A. & Butler, A. B. (2005) Avian brains and a new understanding of vertebrate brain evolution. *Nature Reviews Neuroscience* 6:151–59.
- JERISON, H. J. (1973) *Evolution of the Brain and Intelligence*, New York, Academic Press.
- JOLLY, A. (1966) Lemur social behaviour and primate intelligence. *Science*, 153, 501–506.

- JONES, T. B. & KAMIL, A. C. (1973) Tool-making and tool-using in the northern blue jay. *Science*, 1076-1078.
- JUNIPER, T. & PARR, M. (2003) *Parrots: a guide to the parrots of the world* Christopher Helm, London.
- JURASZ, C. M. & JURASZ, V. P. (1979) Feeding modes of the humpback whale *Megaptera novaeangliae* in Southeastern Alaska USA. *Scientific Reports of the Whales Research Institute Tokyo*, 69-84.
- KAMIL, A. C., JONES, T. B., PIETREWICZ, A. & MAULDIN, J. E. (1977) Positive transfer from successive reversal training to learning set in blue jays (*Cyanocitta cristata*). *Journal of Comparative and Physiological Psychology*, 91, 79-86.
- KAMINSKI, J., RIEDEL, J., CALL, J. & TOMASELLO, M. (2005) Domestic goats, *Capra hircus*, follow gaze direction and use social cues in an object choice task. *Animal Behaviour*, 69, 11-18.
- KARIN-D'ARCY, M. R. & POVINELLI, D. J. (2002) Do chimpanzees know what each other see? A closer look. *International Journal of Comparative Psychology*, 21-54.
- KATZIR, G. (1982) Relationships between social structure and response to novelty in captive jackdaws (*Corvus monedula*), I. Response to novel space. *Behaviour*, 81, 231-264.
- KATZIR, G. (1983) Relationships between social structure and response to novelty in captive jackdaws (*Corvus monedula*), II. Response to novel palatable food. *Behaviour*, 82, 183-207.
- KEETON, W. T. & GOULD, J. L. (1986) *Biological Science*, W.W. Norton & Co Ltd., New York.
- KENDAL, R. L., COE, R. L. & LALAND, K. N. (2005) Age differences in neophilia, exploration, and innovation in family groups of callitrichid monkeys. *American Journal of Primatology*, 66, 167-188.
- KENWARD, B, RUTZ, C, WEIR, A. & KACELNIK, A. (2006) Development of tool use in New Caledonian crows: inherited action patterns and social influences. *Animal Behaviour*, 72, 1329-1343.
- KLÜVER, H. (1933) *Behaviour mechanisms in monkeys* Chicago, University of Chicago Press.
- KÖHLER, W. (1927) *The mentality of apes*, (2nd edn), New York, Vintage Books.
- KRASHENINNIKOVA, A., BRAGER, S. & WANKER, R. (2013) Means-end comprehension in four parrot species: explained by social complexity. *Animal Cognition*, 1-10.
- KRASHENINNIKOVA, A. & WANKER, R. (2010) String-pulling in spectacled parrotlets (*Forpus conspicillatus*). *Behaviour*, 147, 725-739.
- KREBS, J. R., SHERRY, D. F., HEALY, S. D., PERRY, V. H. & VACCARINO, A. L. (1989) Hippocampal specialisation of food-storing birds. *Proceedings of the National Academy of Sciences of the United States of America*, 86, 1388-1392.
- KROODSMA, D. E. & MILLER, E. H. (1996) *Ecology and Evolution of Acoustic Communication in Birds*, Ithaca, NY, Cornell University Press.
- LALAND, K. (2004) Social learning strategies. *Animal Learning & Behaviour*, 32, 4-14.

- LALAND, K. N. & READER, S. M. (1999a) Foraging innovation in the guppy. *Animal Behaviour*, 57, 331-340.
- LALAND, K. N. & READER, S. M. (1999b) Foraging innovation is inversely related to competitive ability in male but not in female guppies. *Behavioural Ecology*, 10, 270-274.
- LEATHERWOOD, S. (1975) Some observations of feeding behaviour of bottle-nosed dolphins (*Tursiops truncatus*) in Northern Gulf-of-Mexico and (*Tursiops cf Tursiops gilli*) off Southern-California, Baja-California, and Nayarit, Mexico. *Marine Fisheries Review*, 37, 10-16.
- LEFEBVRE, L., NICOLAKAKIS, N. & BOIRE, D. (2002) Tools and brains in birds. *Behaviour*, 139, 939-973.
- LEFEBVRE, L., READER, S. M. & SOL, D. (2004) Brains, innovations and evolution in birds and primates. *Brain Behaviour and Evolution*, 63, 233-246.
- LEFEBVRE, L., WHITTLE, P., LASCARIS, E. & FINKELSTEIN, A. (1997) Feeding innovations and forebrain size in birds. *Animal Behaviour*, 53, 549-560.
- LEVINE, M. (1959) A model of hypothesis behaviour in discrimination learning set. *Psychological Review*, 66, 353-366.
- LEVINE, M. (1965) Hypothesis behaviour. IN SCHRIER, A. M., HARLOW, H. P. & STOLLNITZ, F. (Eds.) *Behaviour in Non-human Primates*. NY, Academic Press.
- LEWONTIN, R. C. (1998) The evolution of cognition: Questions we will never answer IN SCARBOROUGH, D. & STERNBERG, S. (Eds.) *An Invitation to Cognitive Science: Methods, Models and Conceptual Issues* Cambridge, MA: MIT Press.
- LIEDTKE, J., WERDENICH, D., GAJDON, G. K., HUBER, L. & WANKER, R. (2010) Big brains are not enough: performance of three parrot species in the trap-tube paradigm. *Animal Cognition*, 14, 143-149.
- LOCKIE, J. D. (1955) The breeding and feeding of jackdaws and rooks with notes on carrion crows and other corvidae. *Ibis*, 97, 341—368.
- LONSDORF, E. V. (2006) What is the role of mothers in the acquisition of termite-fishing behaviours in wild chimpanzees (*Pan troglodytes schweinfurthii*)? *Animal Cognition*, 9, 36-46.
- MACINTOSH, N. J., MCGONIGLE, B., HOLGATE, V. & VANDERVER, V. (1968) Factors underlying improvement in serial reversal learning. *Canadian Journal Of Psychology/Revue Canadienne De Psychologie*, 22, 85-95.
- MACKINTOSH, N. J. (1965) Overtraining, reversal, and extinction in rats and chicks. *Journal of Comparative and Physiological Psychology*, 59, 31-36.
- MACKINTOSH, N. J. (1988) Approaches to the study of animal intelligence. *British Journal of Psychology*, 79, 509.
- MACKINTOSH, N. J. & HOLGATE, V. (1969) Serial reversal training and nonreversal shift learning. *Journal of Comparative and Physiological Psychology*, 67.
- MACPHAIL, E. M. (1982) *Brain and intelligence in vertebrates*, Oxford, England, Clarendon Press.
- MACPHAIL, E. M. & BARLOW, H. B. (1985) Vertebrate Intelligence: The Null Hypothesis [and Discussion]. *Philosophical Transactions of the Royal Society of London. B, Biological Sciences*, 308, 37-51.

- MAGAT, M. & BROWN, C. (2009) Laterality enhances cognition in Australian parrots. *Proceedings of the Royal Society B-Biological Sciences*, 276, 4155-4162.
- MARINO, L. (1996) What can dolphins tell us about primate evolution? *Evolutionary Anthropology*, 5, 81-86.
- MARINO, L. (2002) Convergence of complex cognitive abilities in cetaceans and primates. *Brain Behaviour and Evolution*, 59, 21-32.
- MARINO, L., CONNOR, R. C., FORDYCE, R. E., HERMAN, L. M., HOF, P. R., LEFEBVRE, L., LUSSEAU, D., MCCOWAN, B., NIMCHINSKY, E. A., PACK, A. A., RENDELL, L., REIDENBERG, J. S., REISS, D., UHEN, M. D., VAN DER GUCHT, E. & WHITEHEAD, H. (2007) Cetaceans have complex brains for complex cognition. *PLoS Biology*, 5, 966-972.
- MARTIN, G. R. (2011) Through Birds' Eyes: insights into avian sensory ecology. *Journal of Ornithology* 153, 23-48
- MARTIN, L. B. I. & FITZGERALD, L. (2005) A taste for novelty in invading house sparrows, *Passer domesticus*. *Behavioural Ecology*, 702-707.
- MARTIN, P. & BATESON, P. (1996) *Measuring Behaviour*, Cambridge, Cambridge University Press.
- MARTIN-ORDAS, G., CALL, J. & COLMENARES, F. (2008) Tubes, tables and traps: great apes solve two functionally equivalent trap tasks but show no evidence of transfer across tasks. *Animal Cognition*, 11, 423-430.
- MARTIN-ORDAS, G., HAUN, D., COLMENARES, F. & CALL, J. (2010) Keeping track of time: evidence for episodic-like memory in great apes. *Animal Cognition*, 13, 331-340.
- MARTIN-ORDAS, G., JAEK, F. & CALL, J. (2012) Barriers and traps: great apes' performance in two functionally equivalent tasks. *Animal Cognition*, 15, 1007-1013.
- MARTUSCELLI, P. (1995) Ecology and conservation of the Red-tailed Amazon (*Amazona brasiliensis*) in south-eastern Brazil. *Bird Conservation International*, 5, 405-420.
- MATHIEU, M., DAUDELIN, N., DAGENAIS, Y. & DECARIE, T. G. (1980) Piagetian causality in 2 house-reared chimpanzees (*Pan troglodytes*). *Canadian Journal of Psychology-Revue Canadienne De Psychologie*, 34, 179-186.
- MATSUZAWA, T. (1994) Field experiments on use of stone tools by chimpanzees in the wild. IN R. WRANGHAM, W. MCGREW, F. DE WAAL & HELTNE, P. (Eds.) *Chimpanzee cultures*. Cambridge, MA, Harvard University Press.
- MAYR, E. (1963) *Animal species and evolution*, Cambridge, MA: Belknap.
- MEEHAN, C. L. & MENCH, J. A. (2002) Environmental enrichment affects the fear and exploratory responses to novelty of young Amazon parrots. *Applied Animal Behaviour Science*, 79, 75-88.
- MENDES, N., HANUS, D. & CALL, J. (2007) Raising the level: orangutans use water as a tool. *Biology Letters*, 3, 453-455.
- MENZEL, E. W., JR. (1963) The Effects of Cumulative Experience on Responses to Novel Objects in Young Isolation-Reared Chimpanzees. *Behaviour*, 21, 1-12.
- METTKE-HOFMANN N, C., EBERT, C., SCHMIDT, T., STEIGER, S. & STIEB, S. (2005) Personality Traits in Resident and Migratory Warbler Species. *Behaviour*, 142, 1357-1375.

- METTKE-HOFMANN N, C., LORENTZEN, S., SCHLICHT, E., SCHNEIDER, J. & WERNER, F. (2009) Spatial Neophilia and Spatial Neophobia in Resident and Migratory Warblers (*Sylvia*). *Ethology*, 115, 482-492.
- METTKE-HOFMANN N, C., ROWE, K. C., HAYDEN, T. J. & CANOINE, V. (2006) Effects of experience and object complexity on exploration in garden warblers (*Sylvia borin*). *Journal of Zoology*, 268, 405-413.
- METTKE-HOFMANN N, C., WINKLER, H., HAMEL, P. B. & GREENBERG, R. (2013) Migratory New World Blackbirds (Icterids) Are More Neophobic than Closely Related Resident Icterids. *PLoS One*, 8, e57565.
- METTKE-HOFMANN N, C., WINKLER, H. & LEISLER, B. (2002) The significance of ecological factors for exploration and neophobia in parrots. *Ethology*, 108, 249-272.
- MIKLOSI, A. (2007) *Dogs: Behaviour, evolution & cognition*, New York, Oxford University Press.
- MIKLOSI, A. & SOPRONI, K. (2006) A comparative analysis of animals' understanding of the human pointing gesture. *Animal Cognition*, 9, 81-93.
- MIKLOSI, A., TOPAL, J. & CSANYI, V. (2004) Comparative social cognition: what can dogs teach us? *Animal Behaviour*, 67, 995-1004.
- MIKOLASCH, S., KOTRSCHAL, K. & SCHLOEGL, C. (2011) African grey parrots (*Psittacus erithacus*) use inference by exclusion to find hidden food. *Biology Letters*
- MILTON, K. (1981) Distribution patterns of tropical plant foods as an evolutionary stimulus to primate mental-development. *American Anthropologist*, 83, 534-548.
- MILTON, K. (1988) Foraging behaviour and the evolution of primate intelligence IN R. P. BYRNE, A. W. (Ed.) *Machiavellian Intelligence*. Oxford, Clarendon press.
- MINVIELLE, F., MILLS, A. D., FAURE, J. M., MONVOISIN, J. L. & GOURICHON, D. (2002) Fearfulness and performance related traits in selected lines of Japanese quail (*Coturnix japonica*). *Poultry Science*, 81, 321-326.
- MOORHOUSE, R. J. (1997) The diet of the North Island kaka (*Nestor meridionalis septentrionalis*) on Kapiti Island. *New Zealand Journal of ecology*, 21: 141-152.
- MORAND-FERRON, J., COLE, E. F., RAWLES, J. E. C. & QUINN, J. L. (2011a) Who are the innovators? A field experiment with 2 passerine species. *Behavioural Ecology*, 22, 1241-1248.
- MORAND-FERRON, J., WU, G.-M. & GIRALDEAU, L.-A. (2011b) Persistent individual differences in tactic use in a producer-scrounger game are group dependent. *Animal Behaviour*, 82, 811-816.
- MULCAHY, N. J. & CALL, J. (2006) Apes save tools for future use. *Science*, 312, 1038-1040.
- MULCAHY, N. J., CALL, J. & DUNBAR, R. I. M. (2005) Gorillas (*Gorilla gorilla*) and Orangutans (*Pongo pygmaeus*) encode relevant problem features in a tool-using task. *Journal of Comparative Psychology*, 119, 23-32.
- MULCAHY, N. J., SCHUBIGER, M. N. & SUDDENDORF, T. T. (2012) Orangutans (*Pongo pygmaeus* and *Pongo abelii*) Understand Connectivity in the Skewered Grape Tool Task. *Journal Of Comparative Psychology*.

- MUNDRY, R. & FISCHER, J. (1998) Use of statistical programs for nonparametric tests of small samples often leads to incorrect P values: examples from Animal Behaviour. *Animal Behaviour*, 56, 256-259.
- NAKAGAWA, S. (2004) A farewell to Bonferroni: the problems of low statistical power and publication bias. *Behavioural Ecology*, 15, 1044-1045.
- NICOLAKAKIS, N., SOL, D. & LEFEBVRE, L. (2003) Behavioural flexibility predicts species richness in birds, but not extinction risk. *Animal Behaviour*, 65, 445-452.
- NICOLSON, N. A. (1986) Infants, mothers, and other females. IN SMUTS, B. B., CHENEY, D. L., SEYFARTH, R. M., WRANGHAM, R. W. & STRUHSAKER, T. T. (Eds.) *Primate Societies*. Chicago, IL, University of Chicago Press.
- NIKEI, Y. (1995) Variations of behaviour of carrion crows (*Corvus corone*) using automobiles as nutcrackers. *Japanese Journal of Ornithology*, 44, 21-35.
- NUNN, C. L. & BARTON, R. A. (2001) Comparative methods for studying primate adaptation and allometry. *Evolutionary Anthropology*, 10, 81-98.
- ORTEGA, J. C. & BEKOFF, M. (1987) Avian Play: Comparative Evolutionary and Developmental Trends. *The Auk*, 104, 338-341.
- OSVATH, M. (2009) Spontaneous planning for future stone throwing by a male chimpanzee. *Current Biology*, 19, R190-R191.
- OSVATH, M. & OSVATH, H. (2008) Chimpanzee (*Pan troglodytes*) and orangutan (*Pongo abelii*) forethought: Self-control and pre-experience in the face of future tool use. *Animal Cognition*, 11, 661-674.
- OVERINGTON, S. E., CAUCHARD, L., CÔTE, K.-A. & LEFEBVRE, L. (2011) Innovative foraging behaviour in birds: What characterises an innovator? *Behavioural Processes*, 87, 274-285.
- PAPINI, M. R. (2002) Pattern and process in the evolution of learning. *Psychological Review*, 109, 186-201.
- PARKER, S. T. & GIBSON, K. R. (1977) Object manipulation, tool use and sensorimotor intelligence as feeding adaptations in cebus monkeys and great apes. *Journal of Human Evolution*, 6, 623-641.
- PEARCE, J. M. (2008) *Animal learning and cognition: An introduction*, Psychology Press.
- PENN, D. C., HOLYOAK, K. J. & POVINELLI, D. J. (2008) Darwin's mistake: Explaining the discontinuity between human and nonhuman minds. *Behavioural and Brain Sciences*, 31, 109-+.
- PENN, D. C. & POVINELLI, D. J. (2007) On the lack of evidence that non-human animals possess anything remotely resembling a 'theory of mind'. *Philosophical Transactions of the Royal Society B-Biological Sciences*, 362, 731-744.
- PEPPERBERG, I. M. (1994) Numerical competence in an African gray parrot (*Psittacus erithacus*). *Journal of Comparative Psychology*, 108, 36-44.
- PEPPERBERG, I. M. (1999) *The Alex studies: cognitive and communicative abilities of grey parrots*, Cambridge, MA, Harvard University Press.
- PEPPERBERG, I. M. (2002) The value of the Piagetian framework for comparative cognitive studies. *Animal Cognition*, 5, 177-182.

- PEPPERBERG, I. M. (2004) "Insightful" string-pulling in grey parrots (*Psittacus erithacus*) is affected by vocal competence. *Animal Cognition*, 7, 263-266.
- PEPPERBERG, I. M. (2006a) Grey parrot numerical competence: A review. *Animal Cognition*, 9, 377-391.
- PEPPERBERG, I. M. (2006b) Grey parrot (*Psittacus erithacus*) numerical abilities: Addition and further experiments on a zero-like concept. *Journal of Comparative Psychology*, 120, 1-11.
- PEPPERBERG, I. M. & FUNK, M. S. (1990) Object permanence in 4 species of *Psittacine* birds: An African grey parrot (*Psittacus erithacus*), an illiger mini macaw (*Ara maracana*), a parakeet (*Melopsittacus undulatus*), and a cockatiel (*Nymphicus hollandicus*). *Animal Learning & Behaviour*, 18, 97-108.
- PEPPERBERG, I. M. & GORDON, J. D. (2005) Number comprehension by a grey parrot (*Psittacus erithacus*), including a zero-like concept. *Journal of Comparative Psychology*, 119, 197-209.
- PEPPERBERG, I. M., KOEPKE, A., LIVINGSTON, P., GIRARD, M. & HARTSFIELD, L. (in press) Reasoning by Inference: Further Studies on Exclusion in Grey Parrots (*Psittacus erithacus*). *Journal of Comparative Psychology*.
- PFUHL, G. (2012) Two strings to choose from: do ravens pull the easier one? *Animal Cognition*, 15, 549-557.
- PIAGET, J. (1953) *Origin of intelligence in the child*, Routledge and Kegan Paul, London.
- PIAGET, J. (1954) *The construction of reality in the child*, Basic Books, New York.
- PINKER, S. (2010) The cognitive niche: Coevolution of intelligence, sociality, and language. *Proceedings of the National Academy of Sciences*, 107, 8993-8999.
- PLATT, M., BRANNON, E., BRIESE, T. & FRENCH, J. (1996) Differences in feeding ecology predict differences in performance between golden lion tamarins (*Leontopithecus rosalia*) and Wied's marmosets (*Callithrix kuhli*) on spatial and visual memory tasks. *Animal Learning & Behaviour*, 24, 384-393.
- POTI, P. & SPINOZZI, G. (1994) Early sensorimotor development in chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*, 108, 93-103.
- POTTS, R. (2004) Paleoenvironmental basis of cognitive evolution in great apes. *American Journal of Primatology*, 62, 209-228.
- POVINELLI, D. J. (2000) *Folk physics for apes. The chimpanzee's theory of how the world works.*, New York, Oxford University Press.
- POVINELLI, D. J. & VONK, J. (2004) We don't need a microscope to explore the chimpanzee's mind. *Mind & Language*, 19, 1-28.
- PRAVOSUDOV, V. V. & CLAYTON, N. S. (2001) Effects of demanding foraging conditions on cache retrieval accuracy in food-caching mountain chickadees (*Poecile gambeli*). *Proceedings of the Royal Society of London Series B-Biological Sciences*, 268, 363-368.
- PRAVOSUDOV, V. V. & DE KORT, S. R. (2006) Is the western scrub-jay (*Aphelocoma californica*) really an underdog among food-caching corvids when it comes to hippocampal volume and food caching propensity? *Brain Behaviour and Evolution*, 67, 1-9.

- PREMACK, D. (2007) Human and animal cognition: Continuity and discontinuity. *Proceedings of the National Academy of Sciences of the United States of America*, 104, 13861-13867.
- PREMACK, D. & PREMACK, A. J. (1994) Levels of causal understanding in chimpanzees and children. *Cognition*, 50, 347-362.
- PREMACK, D. & WOODRUFF, G. (1978) Does the chimpanzee have a theory of mind. *Behavioural and Brain Sciences*, 1, 515-526.
- PRICE, E. E., CALDWELL, C. A. & WHITEN, A. (2010) Comparative cultural cognition. *Wiley Interdisciplinary Reviews: Cognitive Science*, 1, 23-31.
- QUINN, G. P. & KEOUGH, M. J. (2010) *Experimental design and data analysis for biologists*, Cambridge, Cambridge University Press.
- RABY, C. R., ALEXIS, D. M., DICKINSON, A. & CLAYTON, N. S. (2007) Planning for the future by western scrub-jays. *Nature*, 445, 919-921.
- RABY, C. R. & CLAYTON, N. S. (2009) Prospective cognition in animals. *Behavioural Processes*, 80, 314-324.
- RAMSEY, G., BASTIAN, M. & VAN SCHAIK, C. (2007) Animal innovation defined and operationalized. *Behaviour and Brain Science*, 393-437.
- RANGE, F., HORN, L., BUGNYAR, T., GAJDON, G. K. & HUBER, L. (2009) Social attention in keas, dogs, and human children. *Animal Cognition*, 12, 181-192.
- RANGE, F. & NOE, R. (2005) Can simple rules account for the pattern of triadic interactions in juvenile and adult female sooty mangabeys? *Animal Behaviour*, 69, 445-452.
- RAYBURN-REEVES, R. M., LAUDE, J. R. & ZENTALL, T. R. (2013) Pigeons show near-optimal win-stay/lose-shift performance on a simultaneous-discrimination, midsession reversal task with short intertrial intervals. *Behavioural Processes*, 92, 65-70.
- READER, S. & LALAND, K. (2003) Animal Innovation. IN SM, R. & KN, L. (Eds.) *Animal Innovation*. Oxford University Press, Oxford.
- READER, S. M. & LALAND, K. N. (2001) Primate innovation: Sex, age and social rank differences. *International Journal of Primatology*, 22, 787-805.
- READER, S. M. & LALAND, K. N. (2002) Social intelligence, innovation, and enhanced brain size in primates. *Proceedings of the National Academy of Sciences of the United States of America*, 99, 4436-4441.
- REDSHAW, M. (1978) Cognitive-development in human and gorilla infants. *Journal of Human Evolution*, 7, 133-141.
- REHKAMPER, G., FRAHM, H. D. & ZILLES, K. (1991) Quantitative development of brain and brain structures in birds (Galliformes and Passeriformes) compared to that in mammals (insectivores and primates). *Brain Behaviour and Evolution*, 37, 125-143.
- REID, L. S. (1953) The development of noncontinuity behaviour through continuity learning. *Journal of Experimental Psychology*, 46, 107-112.
- REINER, A., PERKEL, D. J., BRUCE, L. L., BUTLER, A. B., CSILLAG, A., KUENZEL, W., MEDINA, L., PAXINOS, G., SHIMIZU, T., STRIEDTER, G., WILD, M., BALL, G. F., DURAND, S., GUNTURKUN, O., LEE, D. W., MELLO, C. V., POWERS, A., WHITE, S. A., HOUGH, G., KUBIKOVA, L., SMULDERS, T. V., WADA, K., DUGAS-FORD, J., HUSBAND, S., YAMAMOTO, K., YU, J., SIANG, C. & JARVIS, E. D. (2004) Revised

- nomenclature for avian telencephalon and some related brainstem nuclei. *Journal of Comparative Neurology*, 473, 377-414.
- RENNER, M. J. (1987) Experience-dependent changes in exploratory behaviour in the adult rat (*Rattus norvegicus*): Overall activity level and interactions with objects. *Journal of Comparative Psychology*, 101, 94-100.
- RICKLEFS, R. E. (2004) The cognitive face of avian life histories. *Wilson Bulletin*, 116, 119-133.
- RIDLEY, M. (1993) *Evolution*, Blackwell Scientific Publications, Inc., Oxford, UK.
- ROSS, C. (2004) Life histories and the evolution of large brain size in great apes. IN RUSSON, A. E. & BEGUN, D. R. (Eds.) *The Evolution of Thought: Evolutionary Origins of great ape intelligence*. Cambridge, Cambridge University Press.
- ROTH, G. & DICKE, U. (2005) Evolution of the brain and intelligence. *Trends in Cognitive Sciences*, 9, 250-257.
- RUMBAUGH, D. (1995) Primate Language and Cognition: Common Ground. *Social Research*, 62, 711-730.
- RUMBAUGH, D. M. (1970) Learning skills of anthropoids. IN ROSEMBLUM, L. A. (Ed.) *Primate Behaviour: Developments in Field and Laboratory Research*. New York, Academic Press.
- RUMBAUGH, D. M. (1971) Evidence of qualitative differences in learning processes among primates. *Journal of Comparative and Physiological Psychology*, 76, 250-255.
- RUMBAUGH, D. M. & PATE, J. L. (1984a) Primates' learning by levels. IN GREENBERG, G. & TOBACH, E. (Eds.) *Behavioural evolution and integrative levels*. Hillsdale, NJ, Lawrence Erlbaum Associates.
- RUMBAUGH, D. M. & PATE, J. L. (1984b) The evolution of cognition in primates: a comparative perspective. IN ROITBLAT, N. H. L., BEVER, T. G. & TERRACE, H. S. (Eds.) *Animal Cognition*. Hillsdale, NJ, Lawrence Erlbaum Associates.
- SALWICZEK, L. H., EMERY, N. J., SCHLINGER, B. & CLAYTON, N. S. (2009) The development of caching and object permanence in Western scrub-jays (*Aphelocoma californica*): Which emerges first? *Journal of Comparative Psychology*, 123, 295-303.
- SANTOS, L., PEARSON, H., SPAEPEN, G., TSAO, F. & HAUSER, M. (2006) Probing the limits of tool competence: Experiments with two non-tool-using species (*Cercopithecus aethiops* and *Saguinus oedipus*). *Animal Cognition*, 9, 94-109.
- SANTOS, L. R., MILLER, C. T. & HAUSER, M. D. (2003) Representing tools: how two non-human primate species distinguish between the functionally relevant and irrelevant features of a tool. *Animal Cognition*, 6, 269-281.
- SANTOS, L. R., ROSATI, A., SPROUL, C., SPAULDING, B. & HAUSER, M. D. (2005) Means-end tool choice in cotton-top tamarins (*Saguinus oedipus*): finding the limits on primates' knowledge of tools. *Animal Cognition*, 8, 236-246.
- SANZ, C., MORGAN, D. & GULICK, S. (2004) New insights into chimpanzees, tools, and termites from the Congo basin. *American Naturalist*, 164, 567-581.

- SCHINO, G., TIDDI, B. & DI SORRENTINO, E. P. (2006) Simultaneous classification by rank and kinship in Japanese macaques. *Animal Behaviour*, 71, 1069-1074.
- SCHLOEGL, C., DIERKS, A., GAJDON, G. K., HUBER, L., KOTRSCHAL, K. & BUGNYAR, T. (2009) What you see is what you get? Exclusion performances in ravens and keas. *PLoS One*, 4, e6368.
- SCHLOEGL, C., KOTRSCHAL, K. & BUGNYAR, T. (2007) Gaze following in common ravens, *Corvus corax*: ontogeny and habituation. *Animal Behaviour*, 74, 769-778.
- SCHLOEGL, C., SCHMIDT, J., BOECKLE, M., WEIS, B. M. & KOTRSCHAL, K. (2012) Grey parrots use inferential reasoning based on acoustic cues alone. *Proceedings of the Royal Society B: Biological Sciences*.
- SCHMIDT, G. F. & COOK, R. G. (2006) Mind the gap: Means-end discrimination by pigeons. *Animal Behaviour*, 71, 599-608.
- SCHNEIDER, L., SERBENA, A. L. & GUEDES, N. M. R. (2002) Manipulação de frutos de acuri e bocaiúva por araras-azuis no Pantanal Sul. *Anais XX Encontro Anual Etol, Natal, Brazil*, 378.
- SCHNEIDER, M. L., MOORE, C. F., SUOMI, S. J. & CHAMPOUX, M. (1991) Laboratory assessment of temperament and environmental enrichment in rhesus monkey infants (*Macaca mulatta*). *American Journal of Primatology*, 25, 137-155.
- SCHRIER, A. M. (1974) Transfer between the repeated reversal and learning set tasks: A reexamination. *Journal of Comparative and Physiological Psychology*, 87, 1004-1010.
- SCHUCK-PAIM, C., ALONSO, W. J. & OTTONI, E. B. (2008) Cognition in an ever-changing world: Climatic variability is associated with brain size in neotropical parrots. *Brain Behaviour and Evolution*, 71, 200-215.
- SCHUCK-PAIM, C., BORSARI, A. & OTTONI, E. B. (2009) Means to an end: Neotropical parrots manage to pull strings to meet their goals. *Animal Cognition*, 12, 287-301.
- SCHULENBERG, T. S., STOTZ, D. F., LANE, D. F., O'NEILL, J. P. & PARKER III, T. A. (2007) *Birds of Peru*, Princetown University Press, US.
- SEED, A., EMERY, N. & CLAYTON, N. (2009a) Intelligence in corvids and apes: A case of convergent evolution? *Ethology*, 115, 401-420.
- SEED, A. M., CALL, J., EMERY, N. J. & CLAYTON, N. S. (2009b) Chimpanzees solve the trap problem when the confound of tool-use is removed. *Journal of Experimental Psychology-Animal Behaviour Processes*, 35, 23-34.
- SEED, A. M., CLAYTON, N. S. & EMERY, N. J. (2007) Postconflict third-party affiliation in rooks, *Corvus frugilegus*. *Current Biology*, 17, 152-158.
- SEED, A. M., TEBBICH, S., EMERY, N. J. & CLAYTON, N. S. (2006) Investigating physical cognition in rooks, *Corvus frugilegus*. *Current Biology*, 16, 697-701.
- SEFERTA, A., GUAY, P. J., MARZINOTTO, E. & LEFEBVRE, L. (2001) Learning differences between feral pigeons and zenaida doves: The role of neophobia and human proximity. *Ethology*, 107, 281-293.
- SEIBT, U. & WICKLER, W. (2006) Individuality in Problem Solving: String Pulling in Two *Carduelis* Species (Aves: Passeriformes). *Ethology*, 112, 493-502.

- SEYFARTH, R. M. & CHENEY, D. L. (1984) Grooming, alliances and reciprocal altruism in vervet monkeys. *Nature*, 308, 541-543.
- SHERWOOD, C. C., SUBIAUL, F. & ZAWIDZKI, T. W. (2008) A natural history of the human mind: tracing evolutionary changes in brain and cognition. *Journal of Anatomy*, 212, 426-454.
- SHETTLEWORTH, S. J. (1993) Where Is the Comparison in Comparative Cognition? Alternative Research Programs. *Psychological Science*, 4, 179-184.
- SHETTLEWORTH, S. J. (2009) The evolution of comparative cognition: Is the snark still a boozum? *Behavioural Processes*, 80, 210-217.
- SHETTLEWORTH, S. J. (2010) *Cognition, Evolution and Behaviour*, Oxford University Press.
- SHULTZ, S., BRADBURY, R. B., EVANS, K. L., GREGORY, R. D. & BLACKBURN, T. M. (2005) Brain size and resource specialisation predict long-term population trends in British birds. *Proceedings of the Royal Society B-Biological Sciences*, 272, 2305-2311.
- SHULTZ, S. & DUNBAR, R. I. M. (2006) Both social and ecological factors predict ungulate brain size. *Proceedings of the Royal Society B: Biological Sciences*, 273, 207-215.
- SHULTZ, S. & DUNBAR, R. I. M. (2007) The evolution of the social brain: Anthropoid primates contrast with other vertebrates. *Proceedings of the Royal Society B-Biological Sciences*, 274, 2429-2436.
- SILK, J. B. (1999) Male bonnet macaques use information about third-party rank relationships to recruit allies. *Animal Behaviour*, 58, 45-51.
- SMOLKER, R. A., RICHARDS, A. F., CONNOR, R. C. & PEPPER, J. W. (1992) Sex-differences in patterns of association among Indian-ocean bottle-nosed dolphins. *Behaviour*, 123, 38-69.
- SOL, D. (2009) Revisiting the cognitive buffer hypothesis for the evolution of large brains. *Biology Letters*, 5, 130-133.
- SOL, D., BACHER, S., READER, S. M. & LEFEBVRE, L. (2008) Brain size predicts the success of mammal species introduced into novel environments. *The American Naturalist*, 172, S63-S71.
- SOL, D., DUNCAN, R. P., BLACKBURN, T. M., CASSEY, P. & LEFEBVRE, L. (2005) Big brains, enhanced cognition, and response of birds to novel environments. *Proceedings of the National Academy of Sciences of the United States of America*, 102, 5460-5465.
- SOL, D. & LEFEBVRE, L. (2000) Behavioural flexibility predicts invasion success in birds introduced to New Zealand. *Oikos*, 90, 599-605.
- SOL, D., SZÉKELY, T. S., LIKER, A. S. & LEFEBVRE, L. (2007) Big-brained birds survive better in nature. *Proceedings of the Royal Society B: Biological Sciences*, 274, 763-769.
- SOL, D., TIMMERMANS, S. & LEFEBVRE, L. (2002) Behavioural flexibility and invasion success in birds. *Animal Behaviour*, 63, 495-502.
- SOMA, M. & HASEGAWA, T. (2004) The Effect of Social Facilitation and Social Dominance on Foraging Success of Budgerigars in an Unfamiliar Environment. *Behaviour*, 141, 1121-1134.

- SPAULDING, B. & HAUSER, M. (2005) What experience is required for acquiring tool competence? Experiments with two callitrichids. *Animal Behaviour*, 70, 517-526.
- SPELKE, E. S. & TSIVKIN, S. (2001) Language and number: A bilingual training study. *Cognition*, 78, 45-88.
- SPENCE, K. W. (1956) *Behaviour theory and conditioning*, New Haven, CT, Yale University Press.
- SPINOZZI, G. & POTI, P. (1993) Piagetian stage 5 in 2 infant chimpanzees (*Pan troglodytes*): The development of permanence of objects and the spatialisation of causality. *International Journal of Primatology*, 14, 905-917.
- SPSS FOR MAC OS X, R. (2007) Chicago: SPSS Inc.
- ST AMANT, R. & HORTON, T. E. (2008) Revisiting the definition of animal tool use. *Animal Behaviour*, 75, 1199-1208.
- STARCK, J. M. (1993) Evolution of avian ontogenies. IN POWER, D. M. (Ed.) *Current Ornithology*. Plenum Press; Plenum Press.
- STARCK, J. M. & RICKLEFS, R. E. (1998) Patterns of development: the altricial-precocial spectrum. IN STARCK, J. M. & RICKLEFS, R. E. (Eds.) *Avian growth and development: evolution within the altricial-precocial spectrum*. Oxford, UK, Oxford University Press.
- STERLENY, K. (2003) *Thought in a Hostile World*, Oxford, Blackwell.
- STRETCH, R. G. A., MCGONIGLE, B. & MORTON, A. (1964) Serial position-reversal learning in the rat: trials/problem and the intertrial interval. *Journal of Comparative and Physiological Psychology*, 57, 461-463.
- STRIEDTER, G. F. (2005) *Principles of brain evolution*, Sunderland, MA, US., Sinauer Associates.
- STÖWE, M., BUGNYAR, T., HEINRICH, B. & KOTRSCHAL, K. (2006a) Effects of Group Size on Approach to Novel Objects in Ravens (*Corvus corax*). *Ethology*, 112, 1079-1088.
- STÖWE, M., BUGNYAR, T., LORETTO, M.-C., SCHLOEGL, C., RANGE, F. & KOTRSCHAL, K. (2006b) Novel object exploration in ravens (*Corvus corax*): Effects of social relationships. *Behavioural Processes*, 73, 68-75.
- SUDDENDORF, T. & CORBALLIS, M. C. (2007) The evolution of foresight: What is mental time travel, and is it unique to humans? *Behavioural and Brain Sciences*, 30, 299-+.
- SUDDENDORF, T. & CORBALLIS, M. C. (2008) New evidence for animal foresight? *Animal Behaviour*, 75, E1-E3.
- SUTHERLAND, N. S. & MACKINTOSH, N. J. (1971) *Mechanisms of animal discrimination learning*, New York, Academic Press.
- TAYLOR, A. H., HUNT, G. R., HOLZHAIDER, J. C. & GRAY, R. D. (2007) Spontaneous metatool use by new Caledonian crows. *Current Biology*, 17, 1504-1507.
- TAYLOR, A. H., HUNT, G. R., MEDINA, F. S. & GRAY, R. D. (2009) Do New Caledonian crows solve physical problems through causal reasoning? *Proceedings of the Royal Society B-Biological Sciences*, 276, 247-254.

- TAYLOR, A. H., MEDINA, F. S., HOLZHAIDER, J. C., HEARNE, L. J., HUNT, G. R. & GRAY, R. D. (2010) An investigation into the cognition behind spontaneous string pulling in new caledonian crows. *PLoS One*, 5, e9345.
- TEBBICH, S., FESSL, B. & BLOMQVIST, D. (2009) Exploration and ecology in Darwin's finches. *Evolutionary Ecology*, 23, 591-605.
- TEBBICH, S., TABORSKY, M., FESSL, B. & DVORAK, M. (2002) The ecology of tool-use in the woodpecker finch (*Cactospiza pallida*). *Ecology Letters*, 5, 656-664.
- THORNTON, A. & RAIHANI, N. J. (2008) The evolution of teaching. *Animal Behaviour*, 75, 1823-1836.
- THORNTON, A. & SAMSON, J. (2012) Innovative problem solving in wild meerkats. *Animal Behaviour*, 83, 1459-1468.
- THORPE, W. H. (1956) *Learning and instinct in animals* London, Methuen and Co.
- TOMASELLO, M. & CALL, J. (1997) *Primate Cognition*, New York, Oxford University Press.
- TOMASELLO, M., CALL, J. & HARE, B. (1998) Five primate species follow the visual gaze of conspecifics. *Animal Behaviour*, 55, 1063-1069.
- TOMASELLO, M., CARPENTER, M., CALL, J., BEHNE, T. & MOLL, H. (2005) Understanding and sharing intentions: The origins of cultural cognition. *Behavioural and Brain Sciences*, 28, 675-735.
- UEHARA, S. (1997) Predation on mammals by the chimpanzee (*Pan troglodytes*). *Primates*, 38, 193-214.
- UZGIRIS, I. C. & HUNT, J. M. V. (1989) *Assessment in infancy: Ordinal scales of psychological development*, University of Illinois Press, Urbana, Ill.
- VAN DE WAAL, E. & BSHARY, R. (2010) Contact with Human Facilities Appears to Enhance Technical Skills in Wild Vervet Monkeys (*Chlorocebus aethiops*). *Folia Primatologica*, 81, 282-291.
- VAN ESSEN, D. C., ANDERSON, C. H. & FELLEMAN, D. J. (1992) Information processing in the primate visual system an integrated systems perspective. *Science*, 255, 419-423.
- VAN HORIK, J. & BURNS, K. C. (2007) Cache spacing patterns and reciprocal cache theft in New Zealand robins. *Animal Behaviour*, 73, 1043-1049.
- VAN HORIK, J., CLAYTON, N. & EMERY, N. (2012) Convergent Evolution of Cognition in Corvids, Apes and Other Animals. IN VONK, J. & SHACKELFORD, T. (Eds.) *Oxford Handbook of Comparative Evolutionary Psychology*. New York, Oxford University Press
- VAN HORIK, J. & EMERY, N. J. (2011) Evolution of cognition. *WIREs: Cognitive Science*, 2, 621-633.
- VAN LAWICK-GOODALL, J. (1968) The behaviour of free-living chimpanzees in the Gombe Stream reserve. *Animal Behaviour Monographs*, 1, 161-311.
- VAN OERS, K., DRENT, P. J., DE GOEDE, P. & VAN NOORDWIJK, A. J. (2004) Realised heritability and repeatability of risk-taking behaviour in relation to avian personalities. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 271, 65-73.
- VAN SCHAIK, C. P., ANCRENAZ, M., BORGAN, G., GALDIKAS, B., KNOTT, C. D., SINGLETON, I., SUZUKI, A., UTAMI, S. S. & MERRILL, M. (2003)

- Orangutan cultures and the evolution of material culture. *Science*, 299, 102-105.
- VAN SCHAİK, C. P., DEANER, R. O. & MERRILL, M. Y. (1999) The conditions for tool use in primates: implications for the evolution of material culture. *Journal of Human Evolution*, 36, 719-741.
- VANDER WALL, S. B. (1990) *Food Hoarding in Animals*, Chicago, Illinois, USA, University of Chicago Press.
- VERBEEK, M. E. M., DRENT, P. J. & WIEPKEMA, P. R. (1994) Consistent individual differences in early exploratory behaviour of male great tits. *Animal Behaviour*, 48, 1113-1121.
- VERVAECKE, H., DE VRIES, H. & VAN ELSACKER, L. (2000) Dominance and its Behavioural Measures in a Captive Group of Bonobos (*Pan paniscus*). *International Journal of Primatology*, 21, 47-68.
- VICK, S. J., BOVET, D. & ANDERSON, J. R. (2010) How do African grey parrots (*Psittacus erithacus*) perform on a delay of gratification task? *Animal Cognition*, 13, 351-358.
- VIRANYI, Z., GACSI, M., KUBINYI, E., TOPAL, J., BELENYI, B., UJFALUSSY, D. & MIKLOSI, A. (2008) Comprehension of human pointing gestures in young human-reared wolves (*Canis lupus*) and dogs (*Canis familiaris*). *Animal Cognition*, 11, 373-387.
- VITALE, A. F., VISALBERGHI, E. & DELILLO, C. (1991) Responses to a snake model in captive crab-eating macaques (*Macaca fascicularis*) and captive tufted capuchins (*Cebus apella*). *International Journal of Primatology*, 12, 277-286.
- VOELKL, B., SCHRAUF, C. & HUBER, L. (2006) Social contact influences the response of infant marmosets towards novel food. *Animal Behaviour*, 72, 365-372.
- VON BAYERN, A. M. P., DE KORT, S. R., CLAYTON, N. S. & EMERY, N. J. (2007) The role of food- and object-sharing in the development of social bonds in juvenile jackdaws (*Corvus monedula*). *Behaviour*, 144, 711-733.
- VON BAYERN, A. M. P. & EMERY, N. J. (2009) Jackdaws respond to human attentional states and communicative cues in different contexts. *Current Biology*, 19, 602-606.
- WALLACE, A. R. (2000) *The Malay archipelago*, Oey, Singapore.
- WALTMAN, J. R. & BEISSINGER, S. R. (1992) Breeding Behaviour of the Green-Rumped Parrotlet. *The Wilson Bulletin*, 104, 65-84.
- WARREN, J. M. (1965) The Comparative Psychology of Learning. *Annual Review of Psychology*, 16, 95-118.
- WARREN, J. M. (1966) Reversal learning and the formation of learning sets by cats and rhesus monkeys. *Journal of Comparative and Physiological Psychology*, 61, 421-428.
- WARREN, J. M., BROOKSHIRE, K. H., BALL, G. G. & REYNOLDS, D. V. (1960) Reversal learning by White Leghorn chicks. *Journal of Comparative and Physiological Psychology*, 53, 371-375.
- WASHBURN, D. A. & RUMBAUGH, D. M. (1991) Rhesus monkey (*Macaca mulatta*) complex learning skills reassessed. *International Journal of Primatology*, 12, 377-388.

- WASSERMAN, E. A. (1993) Comparative cognition - Beginning the 2nd-century of the study of animal intelligence. *Psychological Bulletin*, 113, 211-228.
- WATANABE, S. & CLAYTON, N. S. (2007) Observational visuospatial encoding of the cache locations of others by western scrub-jays (*Aphelocoma californica*). *Journal of Ethology*, 25, 271-279.
- WATTS, D. P. (1998) Coalitionary mate guarding by male chimpanzees at Ngogo, Kibale National Park, Uganda. *Behavioural Ecology and Sociobiology*, 44, 43-55.
- WEBSTER, S. J. & LEFEBVRE, L. (2000) Neophobia by the Lesser-Antillean Bullfinch, a Foraging Generalist, and the Bananaquit, a Nectar Specialist. *The Wilson Bulletin*, 112, 424-427.
- WEBSTER, S. J. & LEFEBVRE, L. (2001) Problem solving and neophobia in a columbiform-passeriform assemblage in Barbados. *Animal Behaviour*, 62, 23-32.
- WEIR, A. A. S., CHAPPELL, J. & KACELNIK, A. (2002) Shaping of hooks in new Caledonian crows. *Science*, 297, 981-981.
- WERDENICH, D. & HUBER, L. (2006) A case of quick problem solving in birds: String pulling in keas, *Nestor notabilis*. *Animal Behaviour*, 71, 855-863.
- WHITEN, A. & BYRNE, R. W. (1988) Tactical deception in primates. *Behavioural and Brain Sciences*, 11, 233-244.
- WHITEN, A., GOODALL, J., MCGREW, W. C., NISHIDA, T., REYNOLDS, V., SUGIYAMA, Y., TUTIN, C. E. G., WRANGHAM, R. W. & BOESCH, C. (1999) Cultures in chimpanzees. *Nature*, 399, 682-685.
- WILSON, B. J., MACKINTOSH, N. J. & BOAKS, R. A. (1985) Transfer of relational rules in matching and oddity learning by pigeons and corvids. *Quarterly Journal of Experimental Psychology*, 37B, 313-332.
- WRANGHAM, R. W. (1999) Evolution of coalitionary killing. *Yearbook of Physical Anthropology*. New York, Wiley-Liss, Inc.
- WURSIG, B. & WURSIG, M. (1980) Behaviour and ecology of the dusky dolphin, *Lagenorhynchus obscurus*, in the South-Atlantic. *Fishery Bulletin*, 77, 871-890.
- YOSEF, R. & YOSEF, N. (2009) Cooperative hunting in brown-necked ravens (*Corvus rufficollis*) on Egyptian Mastiguve (*Uromastyx aegyptius*). *Journal of Ethology*, 385-388.
- ZINKIVSKAY, A., NAZIR, F. & SMULDERS, T. V. (2009) What-Where-When memory in magpies (*Pica pica*). *Animal Cognition*, 12, 119-125.
- ZUCCA, P., MILOS, N. & VALLORTIGARA, G. (2007) Piagetian object permanence and its development in Eurasian jays (*Garrulus glandarius*). *Animal Cognition*, 10, 243-258.