

Running head: NUTCRACKER SOCIAL COGNITION

The Social Cognitive Abilities of the Clark's Nutcracker: From Self to Other

by

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Abstract

This dissertation explored the social cognitive abilities of the Clark's nutcracker (*Nucifraga columbiana*), a relatively non-social, food-caching corvid. Corvids are a family of large-brained birds, which are capable of remarkable cognitive feats (e.g., future planning, tool use). These cognitive abilities have been revealed predominantly by testing social species, supporting popular theories that living in social groups drove the evolution of complex cognition. However, few studies have investigated the social cognitive abilities of corvid species that do not live in large groups. Here, I developed novel procedures using the food-caching behaviour of Clark's nutcrackers as a tool to explore two cognitive abilities predicted to be limited to social species: mirror self-recognition (Chapter 2) and cooperation (Chapter 4). In Chapter 2, birds cached food when alone, with a conspecific present, and with a regular or blurry mirror. The nutcrackers suppressed caching with a regular mirror (as done with a conspecific), but not with the blurry mirror. When integrated with the traditional 'mark test', the birds also showed evidence of self-recognition with the blurry mirror by attempting to remove a coloured mark placed on their body with the blurry mirror, but not with an opaque barrier. In Chapter 3, I discuss the importance of self-recognition as a precursor for complex and flexible social cognitive abilities such as cooperation. To investigate cooperation, in Chapter 4 the birds experienced having their caches exchanged with another bird over multiple trials. This procedure assessed whether the normal response of cache suppression with a conspecific could be over-ridden if the experimental contingencies made cache sharing beneficial. The nutcrackers continued to cache in this context, and male birds increased caching when cooperation from the conspecific was

exaggerated artificially by the experimenter. Combined, the results indicate the non-social Clark's nutcracker is capable of mirror self-recognition, and the ability to distinguish one's 'self' from others may facilitate flexible caching decisions, contrary to the predictions of the social living hypotheses. The findings indicate social living alone does not strongly predict complex cognitive abilities and, instead, that multiple evolutionary paths exist for the development of complex cognition.

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Chapter 1: General Introduction

Imagine living in a large city, a warmer city than Winnipeg of course – a vibrant metropolis of hundreds of thousands, if not millions of people. The streets are bustling and lively. You stroll down a street in a fashionable district, surrounded by and passing people of various shapes, sizes, and colour – each one of them a stranger to you. Though unfamiliar, you quickly access some aspects of their mental experience by observing their facial expressions and gestures. The crowd is mostly jubilant, though you notice a tense pair of faces in serious discussion sitting down at a street-side café patio. As you continue down the street, a cacophony of honks direct your attention to a car stalled on the road, impeding traffic; the driver with a distressed, exasperated look. Before the scene cascades into further road rage, a combination of unrelated bystanders quickly coordinate to help the driver push the car off the road into a nearby parking lot. You see the relieved driver briefly and effervescently thank the rescuers, who promptly continue their anonymous jaunt down the street. As do you – you are meeting a friend for lunch. You quickly assess your appearance, tousling your hair subtly in the reflection of a storefront window, and continue down the street, hoping no one noticed your narcissistic indulgence.

As humans, it seems natural for us to make inferences about the minds of other individuals. As illustrated above, we possess a suite of cognitive abilities that allow us to differentiate the minds of others from our own. Aside from behaviour reading through gesture and facial recognition, we also readily use reflections and understand that our bodies can be represented in an external medium. Not only can we use mirrors in this fashion for judging our physical appearance, we also appreciate that others can perceive us differently than we perceive ourselves. Our ability to understand that our self-

knowledge is distinct from the thoughts and needs of others also seems to allow us to cooperate on a global scale. We maintain societies of strangers and develop technology, whether cars or cellphones, that amplify our ability to coordinate these vast social networks. Witnessing a random act of cooperation as described above, is a common occurrence, not an imaginative invention. The cognitive skills required to maintain such vast social systems seem undeniably impressive. But, how were these cognitive abilities derived through our evolution? Are our complex societies related to, or responsible for, our complex cognitive abilities?

Social Living Hypotheses

To answer such questions about human cognitive evolution some have turned to our closest evolutionary relatives, the non-human primates. The prominent, and long-held, *social function of intellect* hypothesis (Humphrey, 1976), posited that the challenges inherent in social interactions ratcheted up the cognitive skills of primates, including humans, resulting in a general increase in intelligence. Humphrey (1976) was struck by his observation that the most ‘intelligent’ species, namely the great apes and humans, often lived the most mundane lives, devoid of struggle for food or an overwhelming threat of predation, and “could afford to be not only physically but intellectually lazy” (pp. 307). Yet, Humphrey noted that unlike the seemingly undemanding physical environment, the apes’ social environment was a constant source of challenges requiring problem solving. The behaviour of other individuals is often difficult to predict and thus, Humphrey argued that intelligence evolved to solve these social problems and suggested there should be a relationship between social group complexity and intelligence.

Since Humphrey's (1976) influential hypothesis, others have also proposed group living as the key evolutionary promoter of intelligence among animals, most notably, the *Machiavellian intelligence hypothesis* (Byrne & Whiten, 1988; Whiten & Byrne, 1997) and the *social brain hypothesis* (Dunbar, 1998). The *Machiavellian intelligence hypothesis* derived its name from the 16th century philosophical and political teachings of Niccolò Machiavelli who espoused the use of duplicity to maximize political gain from social counterparts. This tactic often required individuals to appear trustworthy and conciliatory, but to abandon these virtues at opportune times for personal advancement. Likewise, the *Machiavellian intelligence hypothesis* suggested a similar evolutionary pressure drove the intelligence of primates – that to maximize fitness, primates needed to maintain the benefits of group living (e.g., antipredator and foraging benefits), while also manipulating their social environment to their advantage (Byrne, 1996). This hypothesis gained notoriety at a time when the social complexity and cognitive sophistication of primates was being increasingly recognized, with reports of using kin support to increase rank (Chapais, 1992), acquiring allies for conflicts through grooming (Cheney, Seyfarth, & Smuts, 1986; Dunbar, 1988; Harcourt, 1988; Smuts, 1985), and providing reconciliation post-conflict to maintain social cohesion (Cords, 1997). Relatedly, the *social brain hypothesis* predicted that with increasing group size there would be a corresponding increase in overall brain size or neocortex size and was buoyed by identified correlations between brain size and social group size in some animal groups (bats: Barton & Dunbar, 1997; carnivores and insectivores: Dunbar & Bever, 1998; cetaceans: Connor, 2007; Marino, 2002; ungulates: Pérez-Barbaría & Gordon, 2005), particularly primates (Barton, 1996; Dunbar, 1992, 1995; Sawaguchi & Kudo, 1990), and

computational evidence that processing power limits group size (Dávid-Barrett & Dunbar, 2013). Indeed, the evidence that group size led to increases in brain size, and presumably more complex cognition, is particularly strong in primates, which show a monotonic relationship between the two variables (Dunbar, 2009). Furthermore, in humans, the brain regions that have expanded the most and gained connectivity over evolutionary time seem to be involved heavily in processing social information (Adolphs, 2009).

Aside from indirect indices of ‘intelligence’ provided by measures of brain volume, when the cognitive abilities of primates are explicitly examined the results often further support for the social living hypotheses. Primates with complex social groups have been at the forefront of research showing them capable of cognitive abilities once thought to be unique to humans, such as tool-use (Povinelli, 2000; van Lawick-Goodall, 1970), metacognition (Smith, Couchman, & Beran, 2012), self-recognition (Gallup, 1970), and social cognition (Hare, Call, Agnetta, & Tomasello, 2000; Hare, Call, & Tomasello, 2001; Povinelli, Neslon, & Boyson, 1990; Premack & Woodruff, 1978).

Based on the convergence of neural and behavioural evidence from primates, many researchers have accepted the basic tenets of the social living hypothesis (Dunbar, 2009) and have since invoked some variant of the social living hypotheses to justify the study of certain species or to explain the cognitive abilities displayed by social species (e.g., dolphins: Marino, 2002; Pack & Herman, 2006; corvids: Bond, Kamil, & Balda, 2003, 2007; Emery & Clayton, 2004, Clayton, Dally, & Emery, 2007; Templeton, Kamil, & Balda, 1999; Tornick, Rushia, & Gibson, 2016; parrots: Krasheninnikova, Bräger, & Wanker, 2013; elephants: Plotnik, de Waal, & Reiss, 2006; Smet & Byrne, 2013).

However, the link between brain size and group size can often be inconsistent outside of primates. For example, the relationship between brain size and group size for insectivores is dependent on whether the species' cerebral development is classified as 'basal' (primitively structured) or 'advanced' (specialized for ecological demands; Dunbar & Bever, 1998). Moreover, phylogenetic analyses of carnivores and ungulates have shown the evolutionary relationship is more readily uncoupled in these groups than with primates (Pérez-Barbaría, Shultz, & Dunbar, 2007), and no relationship between brain and group size has been found for some taxonomic groups such as birds (Beauchamp & Fernandez-Juricic, 2004; Emery, 2004; Iwaniuk & Arnold, 2004) or ungulates (Shultz & Dunbar, 2006). Furthermore, the broad acceptance of the idea that social living is primarily responsible for increases in brain size and cognitive ability across evolutionary time has, in my evaluation, resulted in less emphasis on explicitly examining the cognitive abilities of less social species, limiting the explanatory power of the social living hypotheses.

Corvid Social Cognition

In this dissertation I seek to elucidate the social cognitive abilities of a relatively non-social species, the Clark's nutcracker (*Nucifraga columbiana*), a bird in the corvid family, thereby taking the much-needed step of examining the cognitive abilities of a non-social species. Unlike more social corvids, nutcrackers tend to form small and transient flocks of loosely affiliated juveniles (Hutchins & Lanner 1982; Mewaldt 1948; Tomback 1977; Vander Wall & Hutchins 1983). Males and females typically pair off for the breeding season and aggressively defend their territories from unpaired individuals, who often remain alone instead of joining a flock for the breeding season (Mewaldt

1956). Accordingly, nutcrackers show low intraspecific tolerance, preferring to forage at a distance from others (Tomback 1977), and to make and retrieve caches alone (Tomback 1998). Therefore, several indices place nutcrackers on the non-social end of the spectrum of sociality within corvids, and from a comparative standpoint, this classification makes nutcrackers a valuable species to contrast with more social corvids to evaluate the role of social living on cognitive abilities.

Generally, corvids are characterized by a large brain relative to their body size (Jerison, 1973), particularly with respect to forebrain regions associated with more complex cognitive processes (Lefebvre, Reader, & Sol, 2004; Rehkämper, Frahm, & Zilles, 1991). The increase in brain size differentiates corvids from most other avian species (Cnotka, Güntürkün, Rehkämper, Gray, & Hunt, 2008; Jerison, 1973; Iwaniuk & Nelson, 2003; Emery, Seed, von Bayern, & Clayton, 2007; Rehkämper, et al., 1991), with their relative brain size to body size ratio comparable to that of chimpanzees (Jerison, 1973; Emery, 2006). Not only do corvids have relatively large brains, they also exhibit behaviours indicative of some of the most complex cognitive processing known to occur in non-human animals, mounting a serious challenge to the historic belief of unique primate intelligence (e.g., Humphrey, 1976). Relatively social corvids have been shown to use episodic-like memory (Clayton & Dickinson, 1998) and prospective cognition (Correia, Dickinson, & Clayton, 2007; Raby, Alexis, Dickinson, & Clayton, 2007; Raby & Clayton, 2009) to evaluate when, where, and what to cache, as well as to use transitive inference to assess dominance relationships (Paz-y-mino, Bond, Kamil, & Balda, 2004), accomplishing these types of inferences by a relational rather than an associative representation (Bond et al., 2003; Bond, Wei, & Kamil, 2010; Lazareva et al., 2004;

Lazareva, Smirnova, Zorina, & Rayevsky, 2001). Social corvids have also been shown to have a sophisticated understanding of physical problems (similar to 4-8 year old children: Clayton, 2015) and hidden causality (Taylor, Miller, & Gray, 2012), and have perhaps the most sophisticated tool use and manufacturing abilities among non-human animals (Hunt, 1996; Hunt & Gray, 2006; Weir, Chappell, & Kacelnik, 2002). Furthermore, some social species are capable of mirror self-recognition (Prior, Schwarz, & Güntürkün, 2008) and advanced social cognition resembling Theory of Mind (Bugnyar, 2011; Bugnyar, Reber, & Buckner, 2016; Emery & Clayton, 2001), which has been described as the ‘holy grail’ of comparative cognition research (Povinelli & Vonk, 2003, 2004). Indeed, social cognition is predicted to be particularly well-developed in species with large groups if theories of social living promoting advanced cognitive abilities are accepted.

The advanced social cognition of corvids has in large part been discovered through experiments examining the caching behaviour of corvids. All corvids except for jackdaws and white-throated magpie jays cache food (de Kort & Clayton, 2006). These caches can be stolen by both conspecific (Brockmann & Barnard 1979; Heinrich & Pepper 1998) and heterospecific (Burnell & Tomback, 1985) pilferers. At least for corvid pilferers, stealing caches is aided by their ability to use observational spatial memory to locate cache sites they have witnessed being made (Bednekoff & Balda, 1996a, b). Therefore, to reduce the risk of pilferage, corvids have developed a variety of strategies to protect their caches. Social corvids have been shown to reduce the visual information available to potential pilferers by caching at a distance from other individuals (Bugnyar & Kotrschal, 2002; Dally, Emery, & Clayton, 2005), behind barriers (Bugnyar and Kotrschal, 2002; Dally et al., 2005), in reduced lighting (Dally, Emery, & Clayton, 2004),

or when observers are distracted (Heinrich & Pepper, 1998). The use of deceptive tactics like searching in non-cache locations when observed (Bugnyar & Heinrich, 2006) and making false caches using stones (Clayton & Griffiths, 1994; Heinrich 1999; James & Verbeek, 1983; Kalländer 1978) has also been reported as ways in which social corvids prevent theft of their caches. Finally, some social corvids have been shown to recognize when a caching act has been witnessed and subsequently re-cache the at-risk food to a new location after either chasing the observer away or after the observer has left (Bossema 1979; Dally et al., 2005; Emery & Clayton, 2001; Goodwin 1986; Heinrich, 1999; Wilmore 1977). Engaging in these cache protection behaviours depends on the specific knowledge state (Bugnyar & Heinrich, 2005; Dally, Emery, & Clayton, 2006) and identity of the potential pilferer (Bugnyar & Heinrich, 2006).

Recently, the social cognitive abilities of relatively non-social corvids has been investigated. Clary and Kelly (2011) were the first to show that a non-social corvid engages in cache protection behaviours similar to those documented for social species. Clark's nutcrackers were allowed to cache when alone, within the view of an observer, or with an inanimate object nearby. After caching, the birds in the observed and object conditions had some of their caches pilfered, either by the observing conspecific (observed condition) or artificially by the experimenter (object condition). The nutcrackers responded to being observed by another individual by suppressing their caching. Furthermore, the birds remembered the social conditions in which they cached, as they also recovered more of their caches on a subsequent day if they had previously experienced pilferage. These behavioural changes were not found with the inanimate object, which was made to be as predictive of cache loss as the actual conspecific in the

observed condition, suggesting the behavioural changes were not simply associatively based. That is, even though the object could have acted as an occasion setter signaling that caches would be lost, the birds only perceived a risk to their caches with an animate observer. Subsequent work has since discovered that non-social corvids also prefer to cache at a distance from others (Legg & Clayton, 2016; Tornick et al., 2016), cache behind barriers (Legg & Clayton, 2014), prefer ‘quiet’ caching substrates (Shaw & Clayton, 2013, 2014), and are sensitive to the pilferer’s identity (Kalinowski, Gabriel, & Black, 2015; Shaw & Clayton, 2012). Additionally, non-social corvids may also understand that the knowledge states (Clary & Kelly, 2013; Tornick, Gibson, Kispert, & Wilkinson, 2011) and desire states (Ostojić, Shaw, Cheke, & Clayton, 2013; Ostojić et al., 2014) of others may differ from their own.

The Next Step

The research in this dissertation furthers this line of inquiry by presenting a non-social corvid species with perhaps the most cognitively challenging of social tasks used to date. That is, Clark’s nutcrackers were examined for the ability to recognize their mirror image and the ability to reciprocally cooperate during an iterated prisoner’s dilemma game. For both cognitive domains, I used the nutcrackers’ naturally occurring caching behaviour as a tool to understand their cognition. Self-recognition and cooperation were chosen because they are presumed to require complex cognition, only capable by large-brained and social species (e.g., Bekoff & Sherman, 2004; Stevens & Hauser, 2004), and have been described as a core tenet of the social living hypotheses (Byrne & Whiten, 1997). Thus, if social species have a cognitive advantage, as supposed by the social living

hypotheses, then a non-social species would not be expected to succeed in these most cognitively challenging of social tasks.

In Chapter 2, I examined whether Clark's nutcrackers are capable of mirror self-recognition. To do so, I developed a novel mirror-caching task – during which the birds cached alone, with an observer, and with either a regular mirror or blurry mirror – and then integrated this procedure with the traditional mark test. Therefore, if the birds are able to self-recognize, then they should not suppress caching (as is done with a conspecific) when in the presence of the mirrors. Most of the evidence for self-recognition in non-human animals comes from the mark test developed by Gallup (1970). During Gallup's seminal study, chimpanzees' self-directed behaviours were measured when they were initially exposed to a mirror. Subsequently, during the crucial test phase, the chimpanzees were anesthetized so that a coloured mark could be inconspicuously placed on the subject's forehead. Once recovered, the chimpanzees were given a second exposure to the mirror. The chimpanzees were found to increase inspections to the mark region compared to inspections to the same body locations during baseline. Results from this study were claimed as evidence for self-recognition, and more controversially, self-awareness (Gallup, 1998; Suddendorf & Butler, 2013). Further comparative research has reported that other great apes pass the mark test (Gallup et al., 1995), as well as some large-brained social mammals (Plotnik et al., 2006; Reiss & Marino, 2001) and one species of social corvid (Prior et al., 2008). However, considerable evidence suggests monkeys and lesser apes cannot pass the mark test (Anderson & Gallup, 2015), indicating mirror self-recognition, at least as expressed in the mark test, is limited by a combination of the cognitive capabilities of a species, and perhaps, their sociality. Therefore, self-

recognition can be used as an informative bellwether for the evolutionary emergence of complex cognitive abilities. By testing a non-social corvid I can evaluate whether the previously documented social cognition abilities of nutcrackers are accompanied by a sense of self, lending support to the idea that self-recognition is a necessary prerequisite for more sophisticated social cognition (Baron-Cohen, 1995; Byrne, 1995; Whiten 1996), or whether the reported cache protection behaviours of nutcrackers are indicative of innate species-typical responses, devoid of social cognitive control.

Following Chapter 3, a short linking section, in Chapter 4 I again developed a novel procedure to further examine whether the cache protection strategies of Clark's nutcrackers are stereotyped species-specific responses, or whether the birds can flexibly adjust their caching behaviour to an atypical social context. That is, are nutcrackers able to overcome their typical response of cache suppression in the presence of conspecifics (Clary & Kelly, 2011; Tomback, 1998), when caching in a cooperative context? Thus, pairs of nutcrackers were allowed to cache, but instead of receiving their own caches to retrieve, the birds always exchanged caches with the other bird. The *social competence hypothesis* (Bshary & Oliviera, 2015) argues that social behaviours evolved to be flexible so as to be able to adjust to a constantly changing social world. Therefore, if this hypothesis is correct, then the nutcrackers should recognize the cooperative potential of the task and continue to cache when in the presence of a partner, rather than suppressing their caching behaviour as a cache protection tactic. By testing nutcrackers with this cooperative task that requires the birds to overcome a species-typical response, I can evaluate whether non-social species show flexible social cognition, and thereby test the validity of the *social competence hypothesis* for non-social species. As such, like self-

recognition, cooperation can be used as an indicator of cognitive abilities advanced enough to allow individuals flexibility in their social decisions, and examining a non-social species can provide evidence to assess the importance of social living on this cognitive flexibility.

Combined, these research chapters will give further insight into the validity of the popular social living hypotheses by testing the cognitive abilities of a non-social species in perhaps the most challenging of social tasks to date. The results of these chapters will be placed in the context of the ongoing discussion of the ecological factors that influence brain size and cognitive abilities.

References

- Adolphs, R. (2009). The social brain: neural basis of social knowledge. *Annual Review of Psychology*, *60*, 693–716. doi:10.1146/annurev.psych.60.110707.163514
- Anderson, J. R., & Gallup, Jr, G. G. (2015). Mirror self-recognition: a review and critique of attempts to promote and engineer self-recognition in primates. *Primates*, *56*(4), 317–326. doi:10.1007/s10329-015-0488-9
- Baron-Cohen, S. (1995). *Mindblindness: an Essay on Autism and Theory of Mind*. Cambridge, MA: MIT Press.
- Barton, R. A. (1996). Neocortex size and behavioural ecology in primates. *Proceedings of the Royal Society of London B: Biological Sciences*, *263*, 173-177.
- Barton, R. A., & Dunbar, R. I. M. (1997). Evolution of the social brain. In A. Whiten & R. W. Byrne (Eds.), *Machiavellian intelligence II* (pp. 240–263). Cambridge, UK: Cambridge University Press.
- Beauchamp, G., & Fernández-Juricic, E. (2004). Is there a relationship between forebrain size and group size in birds? *Evolutionary Ecology Research*, *6*(6), 833–842.
- Bednekoff, P. A., & Balda, R. P. (1996). Observational spatial memory in Clark's nutcrackers and Mexican jays. *Animal Behaviour*, *52*, 833–839.
- Bednekoff, P. A., & Balda, R. P. (1996). Social caching and observational spatial memory in pinyon jays. *Behaviour*, 807–826.

- Bekoff, M., & Sherman, P. W. (2004). Reflections on animal selves. *Trends in Ecology and Evolution*, *19*(4), 176–180. doi:10.1016/j.tree.2003.12.010
- Bond, A. B., Kamil, A. C., & Balda, R. P. (2003). Social complexity and transitive inference in corvids. *Animal Behaviour*, *65*(3), 479–487.
doi:10.1006/anbe.2003.2101
- Bond, A. B., Kamil, A. C., & Balda, R. P. (2007). Serial reversal learning and the evolution of behavioral flexibility in three species of North American corvids (*Gymnorhinus cyanocephalus*, *Nucifraga columbiana*, *Aphelocoma californica*). *Journal of Comparative Psychology*, *121*(4), 372–9. doi:10.1037/0735-7036.121.4.372
- Bond, A. B., Wei, C. A., & Kamil, A. C. (2010). Cognitive representation in transitive inference: A comparison of four corvid species. *Behavioural Processes*, *85*(3), 283–292. doi:10.1016/j.beproc.2010.08.003
- Bossema, I. (1979). Jays and oaks: an eco-ethological study of a simbiosis. *Behaviour*, *70*, 1–117.
- Brockmann, H. J., & Barnard, C. J. (1979). Kleptoparasitism in birds. *Animal Behaviour*, *27*, 487–514.
- Bshary, R., & Oliveira, R. F. (2015). Cooperation in animals: toward a game theory within the framework of social competence. *Current Opinion in Behavioral Sciences*, *3*, 31–37. doi:10.1016/j.cobeha.2015.01.008

Bugnyar, T. (2011). Knower-guesser differentiation in ravens: others' viewpoints matter.

Proceedings of the Royal Society B: Biological Sciences, 278, 634-640.

doi:10.1098/rspb.2010.1514

Bugnyar, T., & Heinrich, B. (2005). Ravens, *Corvus corax*, differentiate between

knowledgeable and ignorant competitors. *Proceedings of the Royal Society B:*

Biological Sciences, 272(1573), 1641–1646.

Bugnyar, T., & Heinrich, B. (2006). Pilfering ravens, *Corvus corax*, adjust their

behaviour to social context and identity of competitors. *Animal Cognition*, 9(4),

369–376.

Bugnyar, T., & Kotrschal, K. (2002). Observational learning and the raiding of food

caches in ravens, *Corvus corax*: is it “tactical” deception? *Animal Behaviour*, 64(2),

185–195. doi:10.1006/anbe.2002.3056

Bugnyar, T., Reber, S. A., & Buckner, C. (2016). Ravens attribute visual access to unseen

competitors. *Nature Communications*, 7, 10506. doi:10.1038/ncomms10506

Burnell, K. L., & Tomback, D. F. (1985). Stellar's jays steal gray jay caches: field and

laboratory observations. *Auk* 102, 417–419.

Byrne, R. W. (1995). *The Thinking Ape: Evolutionary Origins of Intelligence*. Oxford,

England: Oxford University Press.

Byrne, R. W. (1996). Machiavellian intelligence. *Evolutionary Anthropology: Issues,*

News, and Reviews, 5(5), 172–180.

- Byrne, R. W., & Whiten, A. (1988). *Machiavellian Intelligence: Social Expertise and the Evolution of Intellect in Monkeys, Apes and Humans*. Oxford, England: Clarendon Press.
- Byrne, R. W., & Whiten, A. (1997). Machiavellian intelligence. In A. Whiten & R. W. Byrne (Eds.), *Machiavellian intelligence II*. Cambridge, UK: Cambridge University Press.
- Chapais, B. (1992). The role of alliances in social inheritance of rank among female primates. In A. H. Harcourt & F. B. M. de Waal (eds.), *Coalitions and Alliances in Humans and Other Primates*, (pp. 29-59). Oxford, England: Oxford University Press.
- Cheney, D. L., Seyfarth, R. M., & Smuts, B. B. (1986). Social relationships and social cognition in nonhuman primates. *Science* 234, 1361-1366.
- Clary, D., & Kelly, D. M. (2011). Cache protection strategies of a non-social food-caching corvid, Clark's nutcracker (*Nucifraga columbiana*). *Animal Cognition*, 14, 735–744. doi:10.1007/s10071-011-0408-3
- Clary, D., & Kelly, D. M. (2013). Are Clark's nutcrackers (*Nucifraga columbiana*) able to discriminate knowledge states of human experimenters during an object-choice task? *Evolutionary Psychology*, 11(3), 628–646.
- Clayton, N. S. (2015). Ways of thinking: From crows to children and back again. *Quarterly Journal of Experimental Psychology*, 68(2), 209–241. doi:10.1080/17470218.2014.943673

- 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(1480), 507–522.
doi:10.1098/rstb.2006.1992
- Clayton, N. S., & Dickinson, A. (1998). Episodic-like memory during cache recovery by scrub jays. *Nature*, 395(6699), 765–768.
- Clayton, N. S., & Griffiths, D. (1994). Storage of stones by jays *Garrulus glandarius*. *Ibis*, 136, 331–334.
- Cnotka, J., Güntürkün, O., Rehkämper, G., Gray, R. D., & Hunt, G. R. (2008). Extraordinary large brains in tool-using New Caledonian crows (*Corvus moneduloides*). *Neuroscience Letters*, 433(3), 241–245.
doi:10.1016/j.neulet.2008.01.026
- 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. doi:10.1098/rstb.2006.1997
- Cords, M. (1997). Friendships, alliances, reciprocity and repair. In A. Whiten & R. W. Byrne (Eds.), *Machiavellian Intelligence II: Extensions and Evaluations*. Cambridge, England: Cambridge University Press.

- 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*(10), 856–61. doi:10.1016/j.cub.2007.03.063
- Dally, J. M., Emery, N. J., & Clayton, N. S. (2004). Cache protection strategies by western scrub-jays (*Aphelocoma californica*): hiding food in the shade. *Proceedings of the Royal Society B: Biological Sciences*, *271 Suppl* (December), S387–90. doi:10.1098/rsbl.2004.0190
- 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*(6), 1251–1263. doi:10.1016/j.anbehav.2005.02.009
- Dally, J. M., Emery, N. J., & Clayton, N. S. (2006). Food-caching Western scrub-jays keep track of who was watching when. *Science*, *312*(5780), 1662–1665. doi:10.1126/science.1126539
- Dávid-Barrett, T., & Dunbar, R. I. M. (2013). Processing power limits social group size: computational evidence for the cognitive costs of sociality. *Proceedings of the Royal Society B: Biological Sciences*, *280*(1765), 20131151. doi:10.1098/rspb.2013.1151
- de Kort, S. R., & Clayton, N. S. (2006). An evolutionary perspective on caching by corvids. *Proceedings of the National Academy of Science, USA*, *273*, 417–423.
- Dunbar, R. I. M. (1988). *Primate Social Systems*. London, England: Croom Helm.

- 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). The mating system of Callitrichid primates. I. Conditions for the coevolution of pairbonding and twinning. *Animal Behaviour*, 50, 1057-1070.
- Dunbar, R. I. M. (1998). The social brain hypothesis. *Evolutionary Anthropology*, 6, 178-190.
- Dunbar, R. I. M. (2009). The social brain hypothesis and its implications for social evolution. *Annals of Human Biology*, 36(5), 562-572.
doi:10.1080/03014460902960289
- Dunbar, R. I. M., & Bever, J. (1998). Neocortex size predicts group size in carnivores and some insectivores. *Ethology*, 104, 695-708.
- Emery, N. J. (2004). Are corvids 'feathered apes'? Cognitive evolution in crows, jays, rooks and jackdaws. In S. Watanabe (Ed.) *Comparative analysis of minds* (pp. 181-213). Tokyo, Japan: Keio University Press.
- Emery, N. J. (2006). Cognitive ornithology: the evolution of avian intelligence. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 361(1465), 23-43. doi:10.1098/rstb.2005.1736
- Emery, N. J., & Clayton, N. S. (2001). Effects of experience and social context on prospective caching strategies by scrub jays. *Nature*, 414(6862), 443-446.

- Emery, N. J. & Clayton, N. S. (2004). The mentality of crows. Convergent evolution of intelligence in corvids and apes. *Science*, *306*, 1903–1907.
- Emery, N. J., Seed, A. M., von Bayern, A. M. P., & Clayton, N. S. (2007). Cognitive adaptations of social bonding in birds. *Proceedings of the Royal Society of London: Biological Sciences*, *362*, 489–505.
- Gallup, Jr, G. G. (1970). Chimpanzees: self-recognition. *Science*, *167*(3914), 86–87.
- Gallup, G. G. (1998). Self-awareness and the evolution of social intelligence. *Behavioural Processes*, *42*, 239–247.
- Gallup, G. G. Jr., Povinelli, D. J., Suarez, S. D., Anderson, J. R., Lethmate, J., & Menzel, E. W. Jr. (1995) Further reflections on self-recognition in primates. *Animal Behaviour*, *50*, 1525–1532.
- Goodwin, D. (1986). *Crows of the World*. London, England: British Museum (Natural History) Books.
- Harcourt, A. (1988). Alliances in contests and social intelligence. In R. W. Byrne & A. Whiten (eds.), *Machiavellian Intelligence: Social Expertise and the Evolution of Intellect in Monkeys, Apes and Humans* (pp. 132-152). Oxford, England: Clarendon Press.
- 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*(1), 139–151. doi:10.1006/anbe.2000.1518

Heinrich, B. (1999). *Mind of the Raven*. New York, NY: Harper.

Heinrich, B., & Pepper, J. W. (1998). Influence of competitors on caching behaviour in the common raven, *Covus corax*. *Animal Behaviour*, *56*, 1083–1090.

Humphrey, N. K. (1976). The social function of intellect. In P. P. G. Bateson & R. A. Hinde (Eds.) *Growing points in ethology* (pp. 303–317). Cambridge, UK: Cambridge University Press.

Hunt, G. R. (1996). Manufacture and use of hook-tools by New Caledonian crows. *Nature*, *379*(18), 249–251.

Hunt, G. R., & Gray, R. D. (2006). Tool manufacture by New Caledonian crows: chipping away at human uniqueness. *Acta Zoologica Sinica*, *52*, 622–625.

Hutchins, H. E. & Lanner, R. M. (1982). The central role of Clark's Nutcracker in the dispersal and establishment of whitebark pine. *Oecologia*, *55*, 192–201.

Iwaniuk, A. N., & Arnold, K. E. (2004). Is cooperative breeding associated with bigger brains? A comparative test in the Corvida (Passeriformes). *Ethology*, *110*(3), 203–220.

Iwaniuk, A. N., & Nelson, J. E. (2003). Developmental differences are correlated with relative brain size in birds: a comparative analysis. *Canadian Journal of Zoology*, *81*(12), 1913–1928.

- James, P. C., & Verbeek, N. A. M. (1983). The food storage behaviour of the northwestern crow. *Behaviour* 85, 276–291.
- Jerison, H. J. (1973). *Evolution of the brain and intelligence*. New York, NY: Academic Press.
- Kalinowski, R. S., Gabriel, P. O., & Black, J. M. (2015). Who's watching influences caching effort in wild Steller's jays (*Cyanocitta stelleri*). *Animal Cognition*, 18, 95–98. doi:10.1007/s10071-014-0780-x
- Kalländer, H. (1978). Hoarding in the rook (*Corvus frugilegus*). *Anser Supplement*, 3, 124–128.
- Krasheninnikova, A., Bräger, S., & Wanker, R. (2013). Means-end comprehension in four parrot species: explained by social complexity. *Animal Cognition*, 16(5), 755–764. doi:10.1007/s10071-013-0609-z
- Lazareva, O. F., Smirnova, A. A., Bagozkaja, M. S., Zorina, Z. A., Rayevsky, V. V., & Wasserman, E. A. (2004). Transitive responding in hooded crows requires linearly ordered stimuli. *Journal of the Experimental Analysis of Behavior*, 82(1), 1–19. doi:10.1901/jeab.2004.82-1
- Lazareva, O. F., Smirnova, A. A., Zorina, Z. A., & Rayevsky, V. V. (2001). Hooded crows solve a transitive inference problem cognitively. *Animal Welfare*, 10, S219–S231.

- Lefebvre, L., Reader, S. M., & Sol, D. (2004). Brains, innovations and evolution in birds and primates. *Brain, Behavior and Evolution*, *63*(4), 233–246.
doi:10.1159/000076784
- Legg, E. W., & Clayton, N. S. (2014). Eurasian jays (*Garrulus glandarius*) conceal caches from onlookers. *Animal Cognition*, *17*(5), 1223–6. doi:10.1007/s10071-014-0743-2
- Legg, E. W., Ostojić, L., & Clayton, N. S. (2016). Caching at a distance: a cache protection strategy in Eurasian jays. *Animal Cognition*. Advance online publication.
doi: 10.1007/s10071-016-0972-7
- Marino, L. (2002). Convergence of complex cognitive abilities in cetaceans and primates. *Brain, Behavior and Evolution*, *59*, 21–32.
- Mewaldt, L. R. (1948). *Nesting habits and some general notes on Clark's Nutcracker (Nucifraga columbiana Wilson)* (Master's Thesis). Montana State University, Montana.
- Mewaldt, L. R. (1956). Nesting behavior of the Clark nutcracker. *Condor* *58*, 3–23.
- Ostojić, L., Legg, E. W., Shaw, R. C., Cheke, L. G., Mendl, M., & Clayton, N. S. (2014). Can male Eurasian jays disengage from their own current desire to feed the female what she wants? *Biology Letters*, *10*(3), 20140042. doi:10.1098/rsbl.2014.0042
- Ostojić, L., Shaw, R. C., Cheke, L. G., & Clayton, N. S. (2013). Evidence suggesting that desire-state attribution may govern food sharing in Eurasian jays. *Proceedings of the*

National Academy of Sciences of the United States of America, (25).

doi:10.1073/pnas.1209926110

Pack, A. A., & Herman, L. M. (2006). Dolphin Social Cognition and Joint Attention: Our Current Understanding. *Aquatic Mammals*, 32(4), 443–460.

doi:10.1578/AM.32.4.2006.443

Paz-y-Mino, C., Bond, A. B., Kamil, A. C., & Balda, R. P. (2004). Pinyon jays use transitive inference to predict social dominance. *Nature*, 430, 778–781.

doi:10.1038/nature02720.1.

Pérez-Barbería, F. J., & Gordon, I. J. (2005). Gregariousness increases brain size in ungulates. *Oecologia* 145, 41-52.

Pérez-Barbería, F. J., Shultz, S., & Dunbar, R. I. M. (2007). Evidence for Coevolution of Sociality and Relative Brain Size in Three Orders of Mammals. *Evolution*, 61(12),

2811–2821. doi:10.1111/j.1558-5646.2007.00229.x

Plotnik, J. M., de Waal, F. B. M., & Reiss, D. (2006). Self-recognition in an Asian elephant. *Proceedings of the National Academy of Sciences U.S.A.*, 103, 17053–

17057.

Povinelli, D. J. (2000). *Folk physics for Apes*. Oxford, England: Oxford University Press.

Povinelli, D. J., Nelson, K. E., & Boysen, S. T. (1990). Inferences about guessing and knowing by chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*,

104, 203–210.

- Povinelli, D. J., & Vonk, J. (2003). Chimpanzee minds: suspiciously human? *Trends in Cognitive Sciences*, 7(4), 157–160. doi:10.1016/S1364-6613(03)00053-6
- Povinelli, D. J., & Vonk, J. (2004). We don't need a microscope to explore the chimpanzee's mind. *Mind and Language*, 19(1), 1–28. doi:10.1111/j.1468-0017.2004.00244.x
- Premack, D., & Woodruff, G. (1978). Does the chimpanzee have a theory of mind? *Behavioral and Brain Sciences*, 1(4), 515–526.
- Prior, H., Schwarz, A., & Güntürkün, O. (2008). Mirror induced behavior in the magpie (*Pica pica*): evidence of self-recognition. *PLoS Biology*, 6, e202.
- Raby, C. R., Alexis, D. M., Dickinson, A., & Clayton, N. S. (2007). Planning for the future by western scrub-jays. *Nature*, 445(7130), 919–21. doi:10.1038/nature05575
- Raby, C. R., & Clayton, N. S. (2009). Prospective cognition in animals. *Behavioural Processes*, 80(3), 314–24. doi:10.1016/j.beproc.2008.12.005
- Rehkämper, G., Frahm, H. D., & Zilles, Z. (1991). Quantitative development of brain and brain structures in birds (Galliformes and Passeriformes) compared to that in mammals (insectivores and primates). *Brain, Behavior and Evolution*, 37, 125–143.
- Reiss D. & Marino, L. (2001). Mirror self-recognition in the bottlenose dolphin: a case of cognitive convergence. *Proceedings of the National Academy of Sciences U.S.A.*, 98, 5937–5942.

- Sawaguchi, T., & Kudo, H. (1990) Neocortical development and social-structure in primates. *Primates* 31, 283–289. doi:10.1007/BF02380949
- Shaw, R. C., & Clayton, N. S. (2012). Eurasian jays, *Garrulus glandarius*, flexibly switch caching and pilfering tactics in response to social context. *Animal Behaviour*, 84(5), 1191–1200. doi:10.1016/j.anbehav.2012.08.023
- Shaw, R. C., & Clayton, N. S. (2013). Careful cachers and prying pilferers: Eurasian jays (*Garrulus glandarius*) limit auditory information available to competitors. *Proceedings. Biological Sciences / The Royal Society*, 280(1752), 20122238. doi:10.1098/rspb.2012.2238
- Shaw, R. C., & Clayton, N. S. (2014). Pilfering Eurasian jays use visual and acoustic information to locate caches. *Animal Cognition*, 17(6), 1281–1288. doi:10.1007/s10071-014-0763-y
- 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(1583), 207–15. doi:10.1098/rspb.2005.3283
- Smet, A. F., & Byrne, R. W. (2013). Report African elephants can use human pointing cues to find hidden food. *Current Biology*, 23(20), 2033-2037.
- Smith, J. D., Couchman, J. J., & Beran, M. J. (2012). The highs and lows of theoretical interpretation in animal-metacognition research. *Philosophical Transactions of the*

Royal Society of London. Series B, Biological Sciences, 367(1594), 1297–309.

doi:10.1098/rstb.2011.0366

Smuts, B. B. (1985). *Sex and Friendship in Baboons*. New York, NY: Aldine Hawthorn.

Stevens, J. R., & Hauser, M. D. (2004). Why be nice? Psychological constraints on the evolution of cooperation. *Trends in Cognitive Sciences*, 8(2), 60–625.

doi:10.1016/j.tics.2003.12.003

Suddendorf, T., & Butler, D. L. (2013). The nature of visual self-recognition. *Trends in Cognitive Sciences*, 17(3), 121–127. doi:10.1016/j.tics.2013.01.004

Taylor, A. H., Miller, R., & Gray, R. D. (2012). New Caledonian crows reason about hidden causal agents. *Proceedings of the National Academy of Sciences of the United States of America*, 109(40), 16389–16391. doi:10.1073/pnas.1208724109

Templeton, J. J., Kamil, A. C., & Balda, R. P. (1999). Sociality and social learning in two species of corvids: The pinyon jay (*Gymnorhinus cyanocephalus*) and the Clark's nutcracker (*Nucifraga columbiana*). *Journal of Comparative Psychology*, 113(4), 450–455.

Tomback, D. F. (1977). *The behavioral ecology of the Clark's nutcracker (Nucifraga columbiana) in the eastern Sierra Nevada* (Doctoral dissertation). University of California, California.

Tomback, D. F. (1998). Clark's Nutcracker (*Nucifraga columbiana*). In A. Poole (Ed.), *The birds of North America online*. Ithaca, NY: Cornell Lab of Ornithology.

Retrieved from the Birds of North America online.

<http://bna.birds.cornell.edu/bna/species/331>. doi:10.2173/ bna.331

Tornick, J. K., Gibson, B. M., Kispert, D., & Wilkinson, M. (2011). Clark's nutcrackers (*Nucifraga columbiana*) use gestures to identify the location of hidden food. *Animal Cognition*, *14*(1), 117–125. doi:10.1007/s10071-010-0349-2

Tornick, J. K., Rushia, S. N., & Gibson, B. M. (2016). Clark's nutcrackers (*Nucifraga columbiana*) are sensitive to distance, but not lighting when caching in the presence of a conspecific. *Behavioural Processes*, *123*, 125-133.
doi:10.1016/j.beproc.2015.10.023

Vander Wall, S. B., & Hutchins, H. E. (1983). Dependence of Clark's nutcracker, *Nucifraga columbiana*, on conifer seeds during post fledging period. *The Canadian Field Naturalist*, *97*, 208–214.

van Lawick-Goodall, J. (1970). Tool-using in primates and other vertebrates. *Advances in the Study of Behavior*, *3*, 195–249.

Weir, A. A., Chappell, J., & Kacelnik, A. (2002). Shaping of hooks in New Caledonian crows. *Science*, *297*(5583), 981. doi:10.1126/science.1073433

Whiten, A. (1996). Imitation, pretence, and mindreading: secondary representation in comparative primatology and developmental psychology? In A. E. Russon, K. A. Bard, & S. T. Parker (Eds.). *Reaching into Thought: the Minds of the Great Apes* (pp. 300–324). Cambridge, England: Cambridge University Press.

Whiten, A., & Byrne, R. (1997). *Machiavellian Intelligence II: Extensions and Evaluations*. Cambridge, UK: Cambridge University Press

Wilmore, S. B. (1977). *Crows, Jays, Ravens and Their Relatives*. London, England: David & Charles.

Chapter 2: Graded Mirror Self-Recognition by Clark's Nutcrackers

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People readily recognize themselves in a mirror, a controversial indicator of self-awareness, yet this ability is curiously rare among other animals. The traditionally used ‘mark test’ has shown that some large-brained species are capable of mirror self-recognition¹⁻⁵. During this test a mark is inconspicuously placed on an animal’s body where it can only be seen with the aid of a mirror. If the animal increases the number of actions directed to the mark region when presented with a mirror, the animal is presumed to have recognized the mirror image as its reflection. However, the pass/fail nature of the mark test presupposes self-recognition exists in entirety or not at all. Here, we developed a novel mirror-recognition task, to supplement the mark test, which revealed gradation in the self-recognition ability of Clark’s nutcrackers (*Nucifraga columbiana*), a large-brained bird in the corvid family. To do so, nutcrackers cached food either alone, in front of another nutcracker, or in front of a regular or blurry mirror (to dissociate the visual cues used for self-recognition). We found the nutcrackers suppressed caching with a regular mirror, a behavioural response usually exhibited to prevent cache theft by conspecifics⁶, but did not suppress caching with a blurry mirror. Likewise, during the mark test, most nutcrackers made more self-directed actions to the mark with a blurry mirror than with a regular mirror. Both results indicate self-recognition may be more readily achieved with a blurry mirror and the degree to which a species is able to self-recognize may depend on the visual components available in the reflection. Our approach will promote research examining self-recognition as a graded ability, rather than as an all-or-none response. Breaking down the broad psychological concept of self-recognition into component abilities will facilitate identifying the perceptual, developmental, and evolutionary paths for self-recognition, and complex cognition more generally.

Corvids are a family of large-brained birds recognized for their impressive cognitive abilities, feats that often challenge the notion of unique human or primate cognition^{5,7-9}. Studying the caching behaviour of corvids, in which birds hide food during times of plenty for later retrieval when food is scarce, has revealed many cognitive abilities not previously known¹⁰. In particular, observing interactions between birds caching food and birds trying to steal those caches has highlighted corvids' prowess for social cognition. Indeed, competition for caches likely fuelled an evolutionary arms race between caching and thieving birds, scaffolding the cognitive abilities of corvids¹¹. For example, caching corvids change their strategies for hiding food depending on whether they are observed¹², the identity of the observer¹³⁻¹⁵, and their own experience as thieves^{6,8}. Clark's nutcrackers, for instance, prevent theft by suppressing caching in the presence of conspecific observers⁶ – a finding we capitalized on to study mirror self-recognition.

Evidence of mirror self-recognition in corvids, as expressed in the mark test, is mixed: European magpies passed the mark test⁵; however, a study using jackdaws found no evidence of self-recognition and instead suggested tactile cues provided by the marks, rather than mirror use, best explained the findings from both jackdaws and magpies¹⁶. Given the success of caching paradigms in revealing the cognitive abilities of corvids, we applied this approach to the study of mirror recognition. Because nutcrackers show a social suppression of caching, we explored whether a similar reluctance to cache would occur with a mirror. That is, would the birds view their mirror image as a potential thief and suppress caching, or would they recognize the reflection as themselves and cache freely, as if alone? Thus, we allowed ten mirror-naïve birds to cache alone, with another

nutcracker, and with a regular or blurry mirror over multiple trials (Extended Data Fig. 1). When viewing a mirror, two sources of information can aid self-recognition: identity information gained from fine-scale details, and contingent motion information gained from the correspondence between one's own movements and that of the reflection¹⁷ (i.e., as the individual moves, so does the reflected image in the same direction and time). By applying a film of faux window frosting to a regular mirror to create a blurry mirror, fine details were removed from the reflected image. Therefore, birds could use the contingent motion information provided by the blurry mirror, but not clear identity information. The blurry mirror allowed us to evaluate the roles of identity and contingent motion information: Would removal of identity information disrupt self-recognition through loss of an informative cue or facilitate self-recognition by eliminating cue competition with contingent motion? During each condition, birds were given 45 minutes to eat or cache 50 pine nuts in ice-cube trays filled with sand. Trays were positioned within a double cage so the adjacent cage compartment 'mirrored' the focal bird's compartment.

Relative to caching alone, the nutcrackers suppressed caching when observed by another bird and with the regular mirror (Fig. 1A), indicating the nutcrackers perceived a risk to their caches during these conditions. However, the birds did not suppress caching with the blurry mirror, suggesting the possibility the birds did not interpret the blurred image as a potential thief. To understand the discrepancy between the regular and blurry mirror conditions we further investigated two questions: 1) could the birds learn to self-recognize with a regular mirror, and 2) did the birds self-recognize with the blurry mirror?

To examine whether giving the birds an opportunity to learn the properties of the mirror would allow self-recognition to manifest with the regular mirror, we conducted additional trials using a half mirror covering one vertical side of the testing compartment. The half mirror allowed birds to examine the appearance and disappearance of their reflection at the mirror's edge, though a clear acrylic partition prevented access behind the mirror. Despite this experience, the nutcrackers continued to suppress their caching with the half mirror (Fig. 1B), and preferred to cache on the non-mirror side of the tray (Extended Data Fig. 2). Next, we provided the birds with devoted exposure sessions to mirrors (i.e., no caching trays or partition) on non-test days, during which the birds could explore the adjacent compartment behind the mirror. Even with these sessions cache suppression persisted with the regular mirror (Fig. 1C, Extended Data Fig. 3). Thus, when uncertainty about the identity of the mirror image was paired with the risk of cache theft, the birds were unable to learn to self-recognize with the regular mirror.

To further evaluate how the birds were interpreting the mirror conditions, particularly the blurry mirror, we conducted the traditional mark test after the caching experiments. The birds had a red test mark, a grey plumage-matched control mark, or no mark affixed to the throat region below the beak, outside the bird's normal line of sight (Extended Data Fig. 4). The birds wore these marks during trials with a regular mirror, a blurry mirror, and an opaque barrier with which no self-recognition behaviours should occur (Extended Data Fig. 5). Hence, if the birds are capable of self-recognition, they should show an advantage for identifying the red mark on their body over the grey control mark when exposed to either a regular or blurry mirror.

The birds made more actions to the mark-region with the red test mark than with the grey control mark, but only with the regular and blurry mirrors and not with the opaque barrier (Fig. 2A). Six of the ten birds made more actions to the red mark with the blurry mirror than with the opaque barrier, and one of these birds also used the regular mirror to reliably identify the mark (Fig. 2B, Extended Data Table 1). Therefore, although one bird used the regular mirror to identify the red mark, identification of the red mark was more easily accomplished with the blurry mirror, indicating potential competition between identity and contingent motion information. Importantly, we found no evidence these six birds used tactile cues to detect the mark¹⁶, as the birds did not ruffle their feathers more (a common avian response to remove debris from plumage) when marks were applied (Extended Data Fig. 6). Instead, these six birds used the mirror spontaneously, without explicit training¹⁸, to detect the mark. The other four birds identified the red mark with the opaque barrier indicating this subset of birds could either feel the mark or, more likely, glanced the mark in their peripheral vision when preening (Extended Data Fig. 6), consistent with findings reported for jackdaws¹⁶.

When the mark test results are considered in conjunction with the results of the caching task, we conclude that the birds were interpreting the blurry image as their reflection and not as another individual. Between both tasks, most nutcrackers showed an advantage for self-recognition when in the presence of a blurry mirror. One bird (Fido) showed evidence of self-recognition with both the regular and blurry mirrors. During the caching task, Fido did not suppress caching with either mirror type (though there was also no suppression to an actual conspecific [$M_{Baseline} \pm SEM = 26.67 \pm 3.02$; $M_{Alone} \pm SEM = 23.83 \pm 2.96$; $M_{Mirror} \pm SEM = 24.83 \pm 3.48$; $M_{Blurry} \pm SEM = 25.17 \pm 3.84$; $M_{Observed} \pm SEM =$

23.83 ± 1.94]), and during the mark test, Fido reliably made actions to the mark region only when the red mark, and not the grey mark, was applied during mirror conditions. Therefore, it seems nutcrackers are capable of self-recognition in the sense that they understood their bodies could be represented in an external medium, although learning their specific features proved much more difficult. The results of Fido however, indicate this ability is not outside the capabilities of this species, though the learning history of individuals (i.e., cue competition resulting from reliable natural associations between contingent motion and ‘self’ and between identity information and ‘others’) may bias against learning to self-recognize with high quality reflections. It is still unclear why some individuals of a species are able to overcome this prior learning and others are not – a common feature of most mark test studies, where only a small subset of animals pass the test²⁻⁵.

Although the results are plausible under the self-recognition interpretation, it is possible that the birds did not appreciate that the blurred image was a reflection during the caching task. Possible alternate explanations may be the birds interpreted the image as a conspecific that could not see them well enough to be a risk (i.e., inferring from their own obscured view that the conspecific must also share this degraded view). Another possibility is the birds were unable to extract any perceptual information from the blurred image at all. Both of these alternative explanations would also predict the lack of cache suppression observed during the blurry mirror condition. However, it is unlikely the birds’ understanding of the blurred image changed so fundamentally between caching and mark test contexts, the latter of which strongly suggests the birds used the visual information from the blurry mirror and this information facilitated their identification of

the red test mark, but not the grey control mark. Further testing will certainly be required to confirm this preliminary finding. In particular, an additional caching condition, during which a focal bird caches with an observer placed behind a 'blurred' acrylic barrier, would be a useful control condition for validating the mirror-caching task as a stand-alone measure of self-recognition.

The blurry mirror resembles conditions the birds experience naturally: distorted reflections, such as in water; and self-generated images only containing contingent motion information, such as with shadows. On exposure to a regular mirror, the unfamiliar identity information may interfere with the birds' ability to attend to the more diagnostic contingent motion information required to foster self-recognition. The blurry mirror likely acted as a band-pass filter removing the high spatial frequencies associated with identity information, allowing the birds to attend to contingent motion information through global cues provided by low spatial frequencies¹⁹. Developmental evidence from children has also indicated contingent motion is particularly important for self-recognition²⁰. Therefore, removing identity information may be important for identifying self-recognition as it eliminates competition between identity information, which in nature is highly associated with other individuals and rarely oneself, and contingent motion, which is highly associated with oneself and rarely other individuals. The dissociated use of identity and contingent motion information discovered here undermines previous negative findings with other species examined for mirror use, particularly corvids^{16,21,22}.

Our work advances the study of self-recognition in three important aspects. First, we deviate from the predominant approach of relying solely on the mark test by

supplementing the mark test with a task exploiting an ecologically relevant behaviour (i.e., caching). Using ecologically relevant behaviours has the advantage of more easily tapping into a species' natural cognitive abilities as it ensures the animal engages in behaviour they are motivated to express. Such motivational differences among species for removing marks or interacting with mirrors can interfere with identifying self-recognition^{23,24}. With our approach the animal is not forced into an interaction with a mirror, rather, self-recognition can emerge as a by-product of the animal's social or foraging behaviour. Second, this is the first study to show a corvid self-recognizing during the mark test that cannot be accounted for by the use of tactile cues¹⁶, providing evidence of convergence between the mental abilities of corvids and primates²⁵ and that a mammalian neocortex is not necessary for self-recognition⁵. However, the capacity for self-recognition likely varies by species along an evolutionary gradient according to their ecology. Third, using blurred reflections enables us to examine what visual information is important for self-recognition and provides a potential gradient by which we can assess different species.

Our results suggest the larger psychological construct of self-recognition can be broken into component abilities²⁶, use of identity and contingent motion information²⁷, thereby facilitating more useful comparative evolutionary analyses of this trait²⁸. Thus, instead of limiting self-recognition to a binary, pass/fail decision, we can now add nuance by asking what are the component abilities of mirror self-recognition, what components are present in any given species, and how these components progress throughout development in both human and non-human animals.

Methods

Subjects

Seventeen Clark's nutcrackers (*Nucifraga columbiana*) participated in the experiment: ten focal birds (five female; five male) and seven observers (three male; four female) participated in the experiment. Sample size was based on previous studies to ensure adequate detection power. All focal birds participated in each experiment described. All birds had previous experience in caching experiments, but had no laboratory experience with mirrors. Birds were housed in individual cages (73 x 48 x 48 cm) and fed *ad libitum* on non-experimental days. Observer birds were fed *ad libitum* at all times. Diet consisted of turkey starter, parrot pellets, sunflower seeds, peanuts, pine nuts, mealworms, oyster shells, and a vitamin powder supplement. The colony room was maintained at 21°C and a 12:12 day:night cycle with light onset at 0700. Birds had been housed in the laboratory for 10-16 years. All procedures were approved by the local animal care committee (#F10-029) and in compliance with the standards of the Canadian Council on Animal Care.

Caching Experiments

Apparatus. Birds cached in plastic ice cube trays filled with sand (26 wells arranged in a 13 x 2 matrix; 49.5 x 11.5 cm), placed into each side of a double cage (123 x 63.5 x 66.5 cm) in an isolated experimental room. A wooden dowel perch was placed in the corner of each compartment. The cage was placed on a table surrounded by white curtains to create a uniform viewing environment. Trays were arranged along the cage wall nearest to the adjacent compartment. The double cage (and trays) could be separated by a removable clear acrylic or mirror partition (65 x 62 cm). All trials were recorded

using an EverFocus® 1/3” color digital camera and the motion tracking program, BiObserve.

General procedures. Focal birds were food deprived 24 hours prior to participating in a weekly trial. Each trial consisted of a *Caching Session* and a *Retrieve Session*. On the first day, a bird was placed in one side of the double cage and allowed to eat and cache 50 pine nuts (i.e., *Caching Session*) for 45 minutes. The birds were then returned to the colony room and supplemented with a restricted amount of regular feed to maintain their weight after food deprivation. On the next day, the birds were returned to the experimental cage to recover their caches for 45 minutes (i.e., *Retrieve Session*). If caches remained in the tray or cage after the session, additional sessions were conducted until all caches were recovered. Birds were returned to an *ad libitum* diet after completing the *Retrieve Session*.

Experiment 1: Caching with a blurry mirror. The birds participated in one habituation trial followed by six Baseline trials before experiencing test conditions. After Baseline trials, each bird was given six blocks of test trials, each block consisting of one Alone, Observed, Mirror, and Blurry Mirror trial, conducted in randomized order. For all conditions, the number of pine nuts cached (both in the tray and external) and eaten during the *Caching* and *Retrieve Sessions* was documented.

Baseline/Alone. During Baseline (and the one habituation trial), a clear acrylic partition separated the two cage compartments. The focal bird was placed in one compartment with a caching tray placed along the clear partition. The other compartment contained an identical caching tray placed along the clear partition so that it was parallel with the other tray. This condition assessed each bird’s normal caching when alone and

without cache loss. Alone trials were identical to Baseline, but conducted concurrently with the other test conditions.

Mirror/Blurry Mirror. During this condition, either a regular mirror or a blurry mirror was inserted behind the clear acrylic partition. The blurry mirror was created by covering a mirror with a film of faux window frosting (Artscape Inc. Texture Twelve), such that it obscured fine details, but remained reflective. Once the bird was returned to the colony room after the *Caching Session*, the experimenter artificially pilfered half of the caches made by the focal bird to simulate cache theft.

Observed. An observer bird was placed in the compartment adjacent to the focal bird. Each focal bird was paired with the same observer for the duration of the experiment. All observers were of the same sex and approximate size as the focal bird. Observers were provided with pine nuts to eat and cache, so the focal bird would be exposed to behaviours they would see during the mirror conditions. The focal bird was returned to the colony room first, followed by the observer ten minutes later. This was done to create a period of uncertainty for the focal bird, during which the observer was left alone with the caching trays, though in reality did not have access to the focal bird's tray. As with the mirror conditions, the experimenter artificially pilfered half of the focal bird's caches prior to the *Retrieve Session*.

Experiment 2: Caching with a half mirror. General procedures were identical to Experiment 1, except each bird was given three blocks of test trials, each block consisting of one Alone, Observed, and Half Mirror trial, presented in randomized order. The half mirror (37 x 62 cm) was placed behind the clear acrylic partition so that it covered the left half of the opening between cage compartments. One bird (Reorx) was

paired with a new observer after the second Observed trial due to the unavailability of the original observer.

Experiment 3: Caching after devoted mirror sessions. General procedures were identical to Experiment 1, except each bird was given three blocks of test trials, each block consisting of one Alone, Observed, and Mirror trial, presented in randomized order. Additionally, birds were given 20 minute exposure sessions, during which the birds were individually placed in the experimental cage with just the half mirror, no caching trays, and the clear partition only extended to the edge of the half mirror. Thus, the birds had access to the back of the mirror by entering the adjacent cage compartment. These sessions were conducted on weekdays the birds were not scheduled to participate in either a *Caching* or *Retrieve Session*.

Mark Test

Apparatus. Trials were conducted in the same environment as the previous experiments. Marks were made from coloured adhesive dots (diameter = 6 mm). Grey marks were made to match the nutcracker's plumage by painting them with Ominous Grey (50YR 26/023) CIL® paint. Red marks weighed on average 6325 ± 969 μg ; grey marks weighed on average 7850 ± 814 μg (mean \pm standard deviation).

Procedure. All birds experienced two 20-minute trials each day during which a bird was marked with a red, grey, or sham mark^{5,16}. Before a trial, the experimenters covered the bird's head so a mark could be pressed onto the bird's throat feathers outside the bird's normal range of sight (Extended Data Fig. 4). The experimenter then gently pressed on various parts of the bird's body so tactile cues were not exclusive to the mark region. In the case of the sham mark, a mark was pressed onto the bird as described, but

immediately removed before pressing other parts of the body. Next, the bird was placed into the cage, where an opaque white barrier, a regular mirror, or a blurry mirror separated the cage compartments. All birds experienced six trials of each condition, two trials with each mark, presented in pseudo-randomized order so birds experienced each condition-mark combination once before repeating any trial type.

Statistical Analysis

For the caching experiments, number of caches was documented after each session. For the mark test, we scored the number of actions (with either a foot or the beak) a bird made to the mark region, to any other part of the plumage, and any feather ruffling (either by shaking the head or shoulders) that could be used to detect disturbances of the plumage. Analysis was based on number of actions rather than proportion of total actions because identifying the mark often stimulated further preening, reducing the proportion of mark actions during successful trials. All trials were scored by DC, and because blinding was not possible during scoring due to the easily distinguishable trial types, a second rater scored a subset of 25 trials as an inter-rater reliability check. The scoring of these behaviours was highly correlated between the two raters ($r = 0.97$). On items of disagreement the two scorers came to a consensus on the correct decision to be used in the final analysis.

Linear mixed-effects models were constructed inputting mirror condition and mark condition (for the mark test) as fixed effects, and subject inputted as a random effect to account for repeated measures taken on each bird. The advantage of using mixed-effects models is that it avoids averaging of each individual's scores, instead, using the entirety of the data and accounting for more sources of variation by allowing for

each individual to have a unique intercept. Therefore, the dependency between scores of individuals, inherent in repeated measures designs, is accounted for by explicitly informing the model that there will be multiple responses per individual (by inputting subject as a random factor) and these responses are allowed to vary according to each individual's baseline intercept²⁹. Residual plots indicated assumptions of normality were valid. No birds were excluded from the analyses, and all birds completed all conditions for a balanced design with similar variances between groups. Analyses were conducted in R version 3.1.2 using the *lme4*³⁰ and *lmerTest* packages³¹. Results from the mixed-effects model were comparable to results produced from more traditional multivariate ANOVA techniques.

References

1. Gallup, G.G., Jr. Chimpanzees: self-recognition. *Science* **167**, 86–87 (1970).
2. Povinelli, D.J., Gallup, G.G., Jr, Eddy, T.J., Bierschwale, D.T., Engstrom, M.C., Perilloux, H.K. & Toxopeus, I.B. Chimpanzees recognize themselves in mirrors. *Anim. Behav.* **53**, 1083–1088 (1997).
3. Plotnik, J.M., de Waal, F.B.M. & Reiss, D. Self-recognition in an Asian elephant. *P. Natl. Acad. Sci. USA* **103**, 17053–17057 (2006).
4. Reiss D. & Marino, L. Mirror self-recognition in the bottlenose dolphin: a case of cognitive convergence. *P. Natl. Acad. Sci. USA* **98**, 5937–5942 (2001).
5. Prior, H., Schwarz, A. & Güntürkün, O. Mirror induced behavior in the magpie (*Pica pica*): evidence of self-recognition. *PLoS Biol.* **6**, e202 (2008).
6. Clary, D. & Kelly, D.M. Cache protection strategies of a non-social food-caching corvid, Clark's nutcracker (*Nucifraga columbiana*). *Anim. Cogn.* **14**, 735-744 (2011).
7. Raby, C., Alexis, D., Dickinson, A. & Clayton, N.S. Planning for the future by western scrub-jays. *Nature* **445**, 919-921 (2007).
8. Emery, N.J. & Clayton, N.S. Effects of experience and social context on prospective caching strategies by scrub jays. *Nature* **414**, 443-446 (2001).
9. Hunt, G. R. Manufacture and use of hook-tools by New Caledonian crows. *Nature* **379**, 249-251 (1996).
10. Grodzinski, U. & Clayton, N. S. Problems faced by food-caching corvids and the evolution of cognitive solutions. *Philos. T. R. Soc. B* **365**, 977–87 (2010).

11. Bugnyar, T. & Kotrschal, K. Observational learning and the raiding of food caches in ravens, *Corvus corax*: is it “tactical” deception? *Anim. Behav.* **64**, 185–195 (2002).
12. Dally, J. M., Emery, N. J. & Clayton, N. S. Cache protection strategies by western scrub-jays, *Aphelocoma californica*: implications for social cognition. *Anim. Behav.* **70**, 1251–1263 (2005).
13. Dally, J. M., Emery, N. J. & Clayton, N. S. Food-caching Western scrub-jays keep track of who was watching when. *Science* **312**, 1662–1665 (2006).
14. Bugnyar, T. & Heinrich, B. Pilfering ravens, *Corvus corax*, adjust their behaviour to social context and identity of competitors. *Anim. Cogn.* **9**, 369–376 (2006).
15. Bugnyar, T. Knower-guesser differentiation in ravens: others’ viewpoints matter. *P. R. Soc. B* **278**, 634-640 (2011).
16. Soler, M., Pérez-Contreras, T. & Peralta-Sánchez, J. M. Mirror-mark tests performed on jackdaws reveal potential methodological problems in the use of stickers in avian mark-test studies. *PloS One*, **9**, e86193 (2014).
17. Parker, S. T. A developmental approach to the origins of self-recognition in great apes. *Hum. Evol.* **6**, 435-449 (1991).
18. Epstein, R., Lanza, R. P. & Skinner, B. F. “Self-awareness” in the pigeon. *Science* **212**, 695-696 (1981).
19. Bar, M. Visual objects in context. *Nat. Rev. Neurosci.* **5**, 617–629 (2004).
20. Povinelli, D. J., Landau, K. R. & Perilloux, H. K. Self-recognition in young children using delayed versus live feedback: evidence of a developmental asynchrony. *Child Dev.* **67**, 1540–1554 (1996).

21. Kusayama, T., Bischof, H. J. & Watanabe, S. Responses to mirror-image stimulation in jungle crows (*Corvus macrorhynchos*). *Anim. Cogn.* **3**, 61–64 (2000).
22. Medina, F. S., Taylor, A. H., Hunt, G. R. & Gray, R. D. New Caledonian crows' responses to mirrors. *Anim. Behav.* **82**, 981–993 (2011).
23. de Veer, M.W. & van den Bos, R. (1999). A critical review of methodology and interpretation of mirror self-recognition research in non-human primates. *Anim. Behav.* **58**, 459-468 (1999).
24. Suddendorf, T. & Butler, D. L. The nature of visual self-recognition. *Trends Cogn. Sci.* **17**, 121–127 (2013).
25. Emery, N. J. & Clayton, N. S. The mentality of crows: convergent evolution of intelligence in corvids and apes. *Science* **306**, 1903–1907 (2004).
26. Rochat, P. Five levels of self-awareness as they unfold early in life. *Conscious. Cogn.* **12**, 717–731 (2003).
27. Kitchen, A., Denton, D. & Brent, L. Self-recognition and abstraction abilities in the common chimpanzee studied with distorting mirrors. *P. Natl. Acad. Sci. USA* **93**, 7405–7408 (1996).
28. Shettleworth, S. J. The evolution of comparative cognition: is the snark still a boojum? *Behav. Process.* **80**, 210–217 (2009).
29. Winter, B. Linear models and linear mixed effects models in R with linguistic applications. arXiv:1308.5499. [<http://arxiv.org/pdf/1308.5499.pdf>] (2013).
30. Bates, D., Maechler, M., Bolker, B & Walker S. lme4: Linear mixed-effects models using Eigen and S4. R package version 1.1-7, <http://CRAN.R-project.org/package=lme4> (2014)

31. Kuznetsova, A., Brockhoff, P.B. & Christensen, R.H.B. lmerTest: Tests in Linear Mixed Effects Models. R package version 2.0-25. <http://CRAN.R-project.org/package=lmerTest> (2015).

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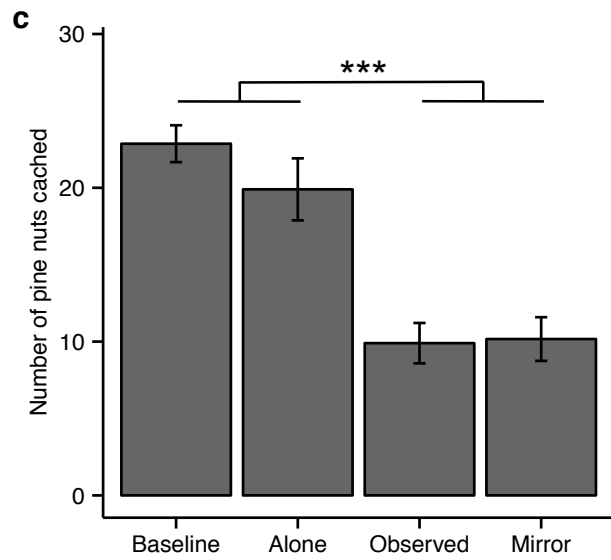
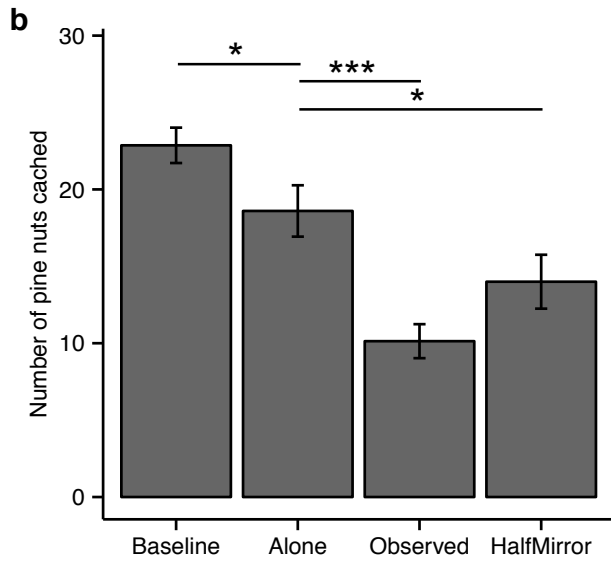
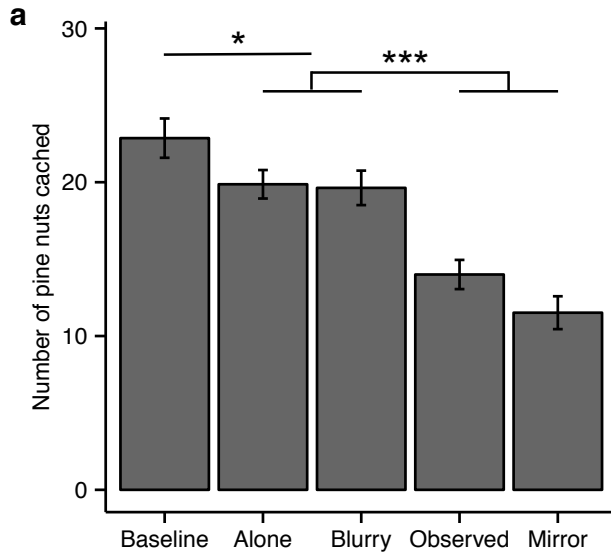


Figure 1. Mean number of pine nuts cached per trial (\pm SEM) by the birds ($n = 10$) during each experiment. a) During experiment 1 examining caching with the blurry mirror, there was an effect of condition ($F_{(4, 286)} = 22.741, p < 0.001$), as the birds cached more when alone than when observed ($t_{(286)} = 4.242, p < 0.001$) or with the regular mirror ($t_{(286)} = 6.038, p < 0.001$), but not the blurry mirror ($t_{(286)} = 0.169, p = 0.866$). Instead, the birds cached more with the blurry mirror than when observed ($t_{(286)} = 4.074, p < 0.001$) or the regular mirror ($t_{(286)} = 5.870, p < 0.001$). b) During experiment 2 examining caching with a half mirror, there was an effect of condition ($F_{(3, 137)} = 21.082, p < 0.001$) with the birds caching more when alone compared to when observed ($t_{(137)} = 4.256, p < 0.001$) or with the half mirror ($t_{(137)} = 2.312, p = 0.022$). c) During experiment 3 examining caching with a full mirror when also given concurrent dedicated mirror exposure trials during non-test days, there was again an effect of condition ($F_{(3, 137)} = 26.816, p < 0.001$) with the birds caching more when alone than with an observer ($t_{(137)} = 4.805, p < 0.001$) or the regular mirror ($t_{(137)} = 4.676, p < 0.001$). Pattern of results was consistent among all three experiments. * $p < 0.05$ *** $p < 0.001$.

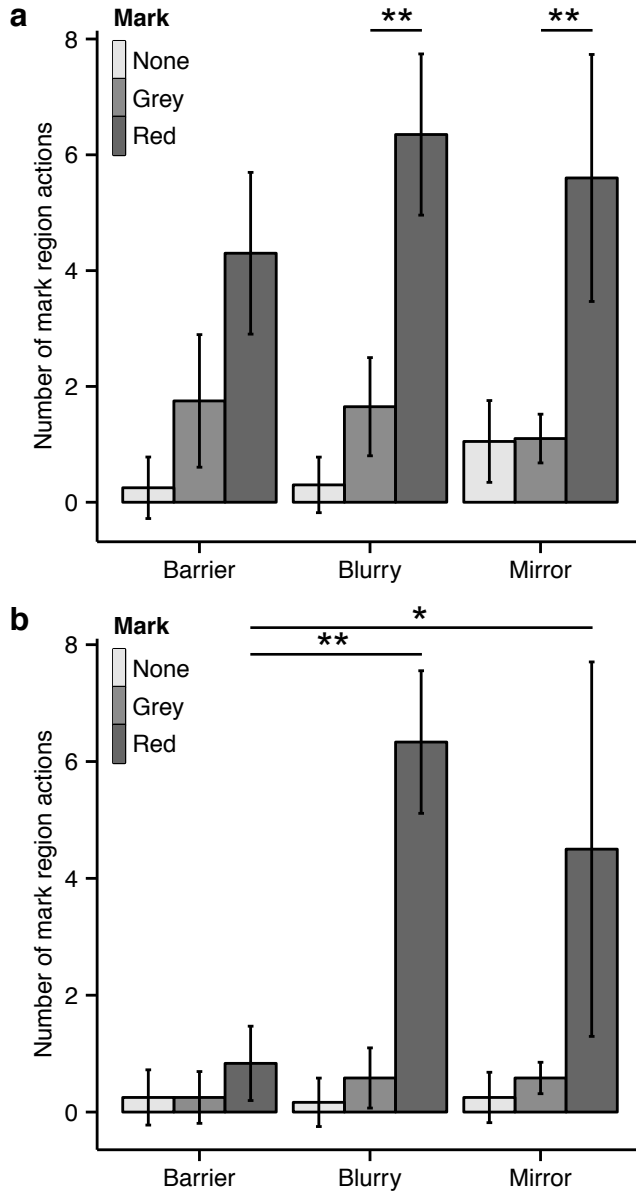


Figure 2. Mean number of actions made to the mark region per trial (\pm SEM) for a) all ten birds and b) the subset of six birds that showed evidence for mirror use. When examining all birds a), there was an effect of mark colour ($F_{(2, 162)} = 16.153, p < 0.001$) as the birds made more mark region actions with the red mark than with the grey mark with the regular mirror ($t_{(162)} = 2.887, p = 0.004$) and blurry mirror ($t_{(162)} = 3.015, p = 0.003$), but not the opaque barrier ($t_{(162)} = 1.636, p = 0.104$). When examining only the six birds

showing mirror use b), there were again more actions to the red mark compared to the other marks ($F_{(2, 94)} = 9.115, p < 0.001$), and the birds made more actions to the red mark with the blurry mirror than with the opaque barrier ($t_{(94)} = 3.309, p = 0.001$). There were also more actions to the red mark with the regular mirror than with the opaque barrier ($t_{(94)} = 2.206, p = 0.030$), though this was largely driven by one individual (Fido; Extended Data Table 1). Pattern of results was consistent with the caching experiments.

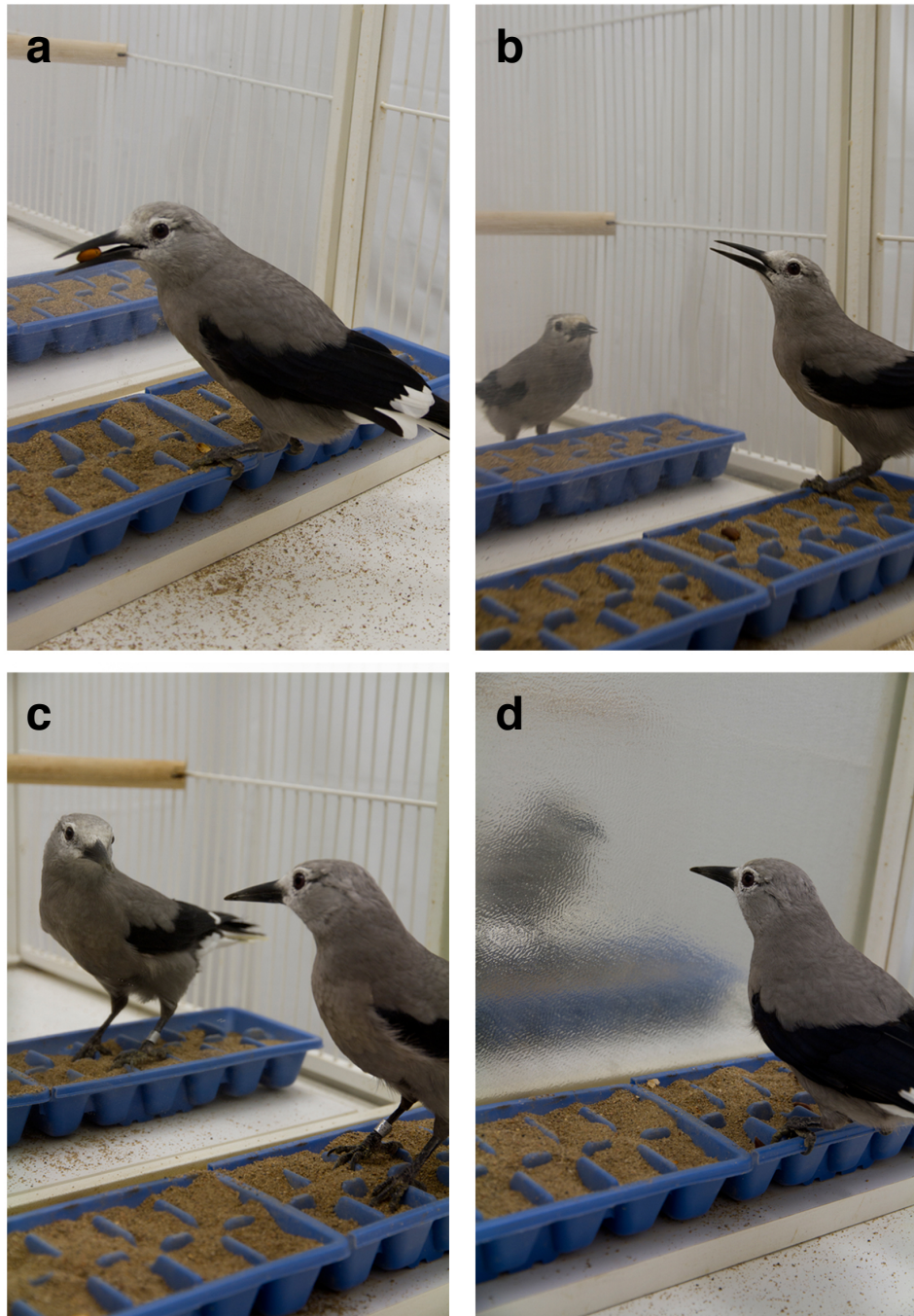
* $p < 0.05$ ** $p < 0.01$.

Extended Data Table 1. **Number of mark actions (trial 1+trial 2) during each condition with each mark**

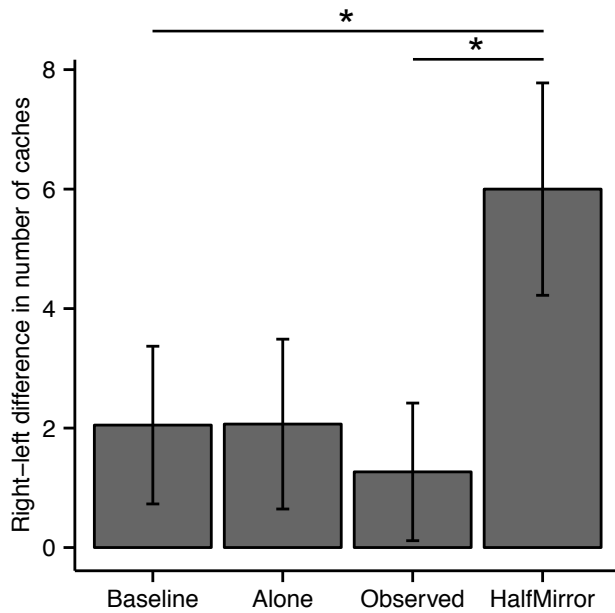
Subject	Barrier /Grey	Barrier /Red	Blurry /Grey	Blurry /Red	Mirror /Grey	Mirror /Red	Regular Mirror	Blurry Mirror	Non-Mirror Visual
Fido	0	0	1	20	5	64	✓	✓	
Bitsy*	0	0	0	19	0	2	✓	✓	
Jan	1	4	0	19	0	3		✓	
Reorx	1	0	1	4	0	0		✓	
Lance	1	1	0	5	2	2		✓	
Capone*	0	5	5	9	0	1		✓	
Krusty*	6	16	20	27	14	18			✓
Sid*	24	22	6	17	0	30			✓
Stefen*	1	10	0	0	1	2			✓
Bert*	1	28	0	7	0	8			✓

Note: Bold values indicate mirror scores that are higher than any control condition.

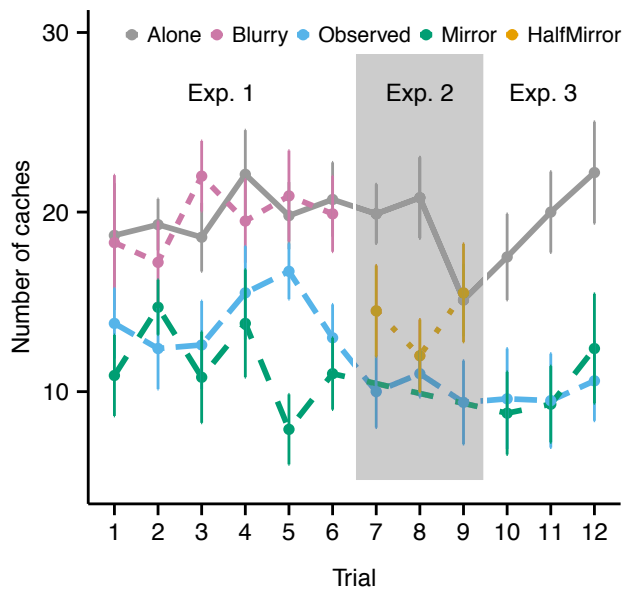
Checkmarks in the Regular and Blurry Mirror columns indicate the bird made 1.5x more mark actions in the mirror condition than in any control condition. Checkmarks in the Non-Mirror Visual column indicate mark actions were elevated during the Barrier/Red condition. Asterisks (*) by the bird names indicate birds that cached at least 1.5x more with the blurry mirror than the regular mirror.



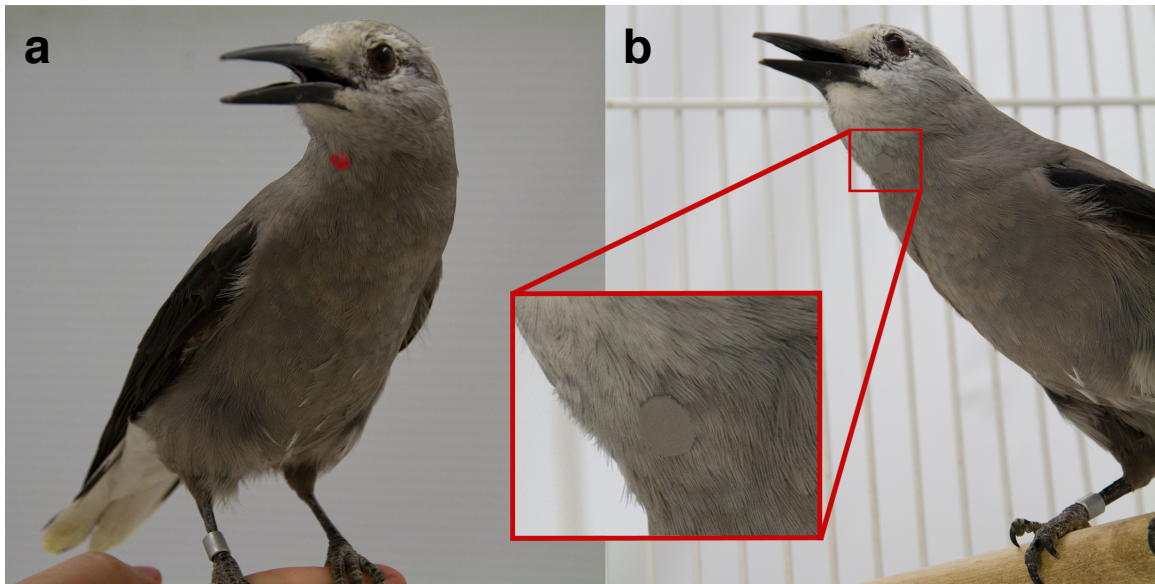
Extended Data Figure 1. Photos showing the a) alone, b) observed, c) regular mirror, and d) blurry mirror caching conditions of Experiment 1.



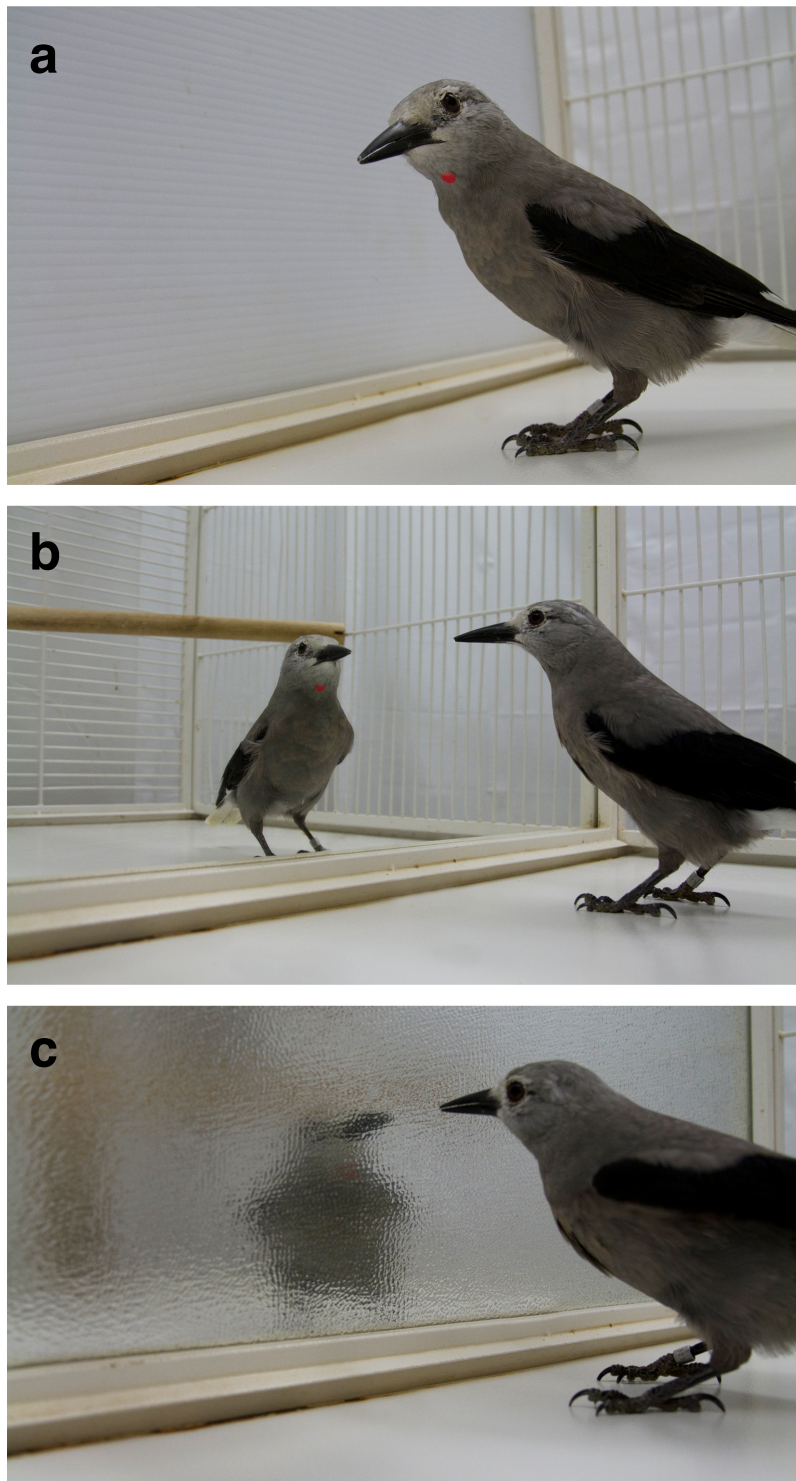
Extended Data Figure 2. Difference between caches made to the non-mirror (right) and mirror (left) sides of the tray (\pm SEM) for all birds ($n = 10$). A stronger preference to cache on the non-mirror side was found during the half mirror trials relative to the baseline ($t_{(137)} = 2.195, p = 0.030$), alone ($t_{(137)} = 1.893, p = 0.061$) and observed ($t_{(137)} = 2.278, p = 0.024$) conditions suggesting the birds were caching away from the visual presence of the reflection. * $p < 0.05$.



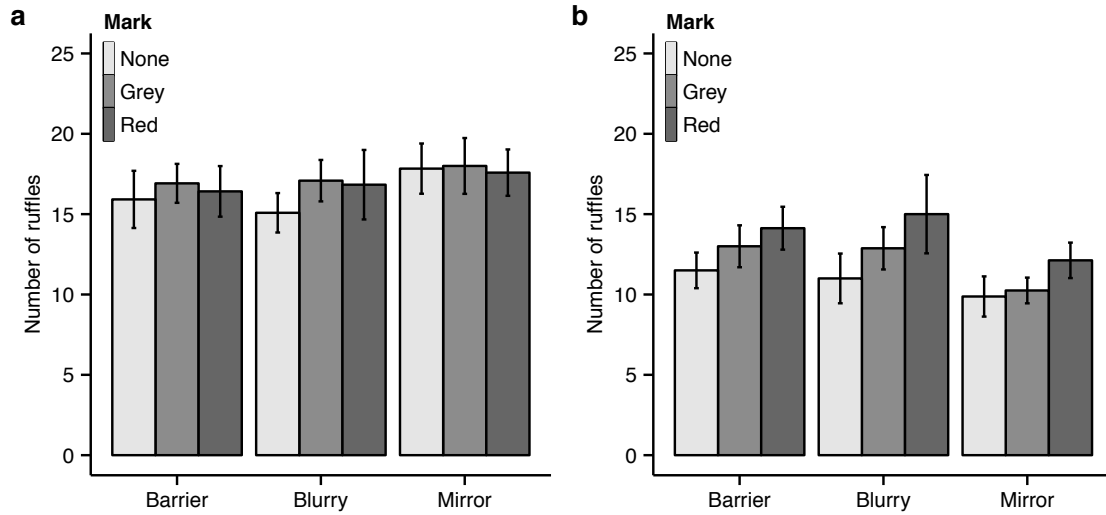
Extended Data Figure 3. Number of caches made (\pm SEM) by the birds ($n = 10$) during each condition over the course of all experiments. The only systematic change was found during the Observed condition which showed a reduction in caching as trials increased ($B = -0.465$, $t_{(401)} = 2.421$, $p = 0.016$).



Extended Data Figure 4. Photos showing the placement of a) red and b) grey marks under the bird's beak. Zoomed image b) is shown to highlight the colour match between the grey mark and the bird's plumage.



Extended Data Figure 5. Photos showing the a) barrier, b) regular mirror, and c) blurry mirror conditions with the red mark.



Extended Data Figure 6. Number of feather ruffles (\pm SEM) across the mirror and mark conditions for a) the six birds showing mirror use, and b) the four birds with no evidence of mirror use. For the six birds showing mirror use a) no effect of mark ($F_{(2,94)} = 0.365$, $p = 0.695$), condition ($F_{(2,94)} = 0.877$, $p = 0.420$), nor any interaction ($F_{(4,94)} = 0.134$, $p = 0.970$) was found for feather ruffling. For the four birds with no evidence of mirror use b) there was only an effect of mark ($F_{(2,60)} = 3.503$, $p = 0.036$) as these four birds ruffled more when wearing a red mark further suggesting mark detection was not overtly mirror-guided, but perhaps more visually-based than tactilely-based.

Chapter 3: From Self to Other

Researchers have proposed self-recognition as a necessary precursor to more sophisticated social cognition processes, such as Theory of Mind (Baron-Cohen, 1995; Byrne, 1995; Whiten 1996). Intuitively, this makes sense as an individual would first need to understand that it has its own distinct thoughts before appreciating that those thoughts are unique and distinct from the thoughts of others. Developmentally, this intuition is supported, as human children develop self-recognition skills earlier (18-24 months: Amsterdam, 1972) than theory of mind skills (36-48 months: Gergely 1994; Gopnik & Meltzoff 1994). Comparatively, species reported to self-recognize, also show behaviours indicative of sophisticated social cognition. Chimpanzees, for example, show a variety of behaviours possibly indicative of mental state attribution (e.g., Hare, Call & Tomasello, 2001; Kaminski, Call & Tomasello, 2008; Byrne & Whiten, 1992). Dolphins perform highly coordinated cooperative hunting and foraging behaviours (Acevedo-Gutierrez, 1999; Connor, Wells, Mann, & Read, 2000; Reynolds, Wells, & Eide, 2000), as well as spontaneously coordinate novel acrobatic patterns in a laboratory setting (Herman, 2002). Elephants are reported to hold funeral-like processions for deceased group members and will return to 'grave' sites even years later (Douglas-Hamilton & Douglas-Hamilton, 1975; Moss 1988; Spinage 1994; McComb, Baker & Moss, 2006). Thus, it may be unsurprising that the nutcrackers possess a sense of self, considering their reported cache protection behaviours.

Given that the nutcrackers show sophisticated social cognition in the form of cache protection strategies (Clary & Kelly, 2011), and understand that their 'self' can be represented by an external reflective surface (Chapter 2), the next question addressed in

this dissertation is whether this self-other distinction affords the birds flexibility in their cognitive strategies. That is, are nutcrackers predisposed to assign certain intentions to other individuals, or can they modulate their behaviour to adjust to an atypical social context?

In the next chapter, nutcrackers were given a cooperative caching task, during which pairs of nutcrackers were allowed to cache, but the caches an individual made were only ever recovered by the other bird. The birds were presented with multiple trials to gain experience with this procedure. Therefore, if the birds understand the cooperative potential of this caching context, I hypothesize that no attempt should be made to protect their caches as the birds learn that maintaining caching behaviour is mutually beneficial. Conversely, if the birds are dominated by an innate tendency to protect caches in the presence of others, then I hypothesize that individuals should show the species-typical response of cache suppression. By examining the caching behaviour of nutcrackers under conditions favourable for cooperation, the importance of sociality for cooperation can be assessed. If the number of group members an individual is likely to interact with is of utmost importance, as follows from the social living hypotheses, then the nutcrackers would not be expected to show cooperative behaviours. If instead, corvids share most cognitive abilities regardless of sociality, and social behaviours are selected to be able to adjust to changing contexts (Bshary & Oliveira, 2015), then nutcrackers should show some degree of flexibility in their caching behaviour to accommodate cooperative decision-making.

References

- Acevedo-Gutierrez, A. (1999). Aerial behavior is not a social facilitator in bottlenose dolphins hunting in small groups. *Journal of Mammalogy*, *80*, 768–776.
- Amsterdam, B. (1972). Mirror self-image reactions before age two. *Developmental Psychobiology*, *5*, 297–305.
- Baron-Cohen, S. (1995). *Mindblindness: an Essay on Autism and Theory of Mind*. Cambridge, MA: MIT Press.
- Bshary, R., & Oliveira, R. F. (2015). Cooperation in animals: toward a game theory within the framework of social competence. *Current Opinion in Behavioral Sciences*, *3*, 31–37. doi:10.1016/j.cobeha.2015.01.008
- Byrne, R. W. (1995). *The Thinking Ape: Evolutionary Origins of Intelligence*. Oxford, England: Oxford University Press.
- Byrne, R. W., & Whiten, A. (1992). Cognitive evolution in primates: evidence from tactical deception. *Man*, *27*, 609-627.
- Clary, D., & Kelly, D.M. (2011). Cache protection strategies of a non-social food-caching corvid, Clark's nutcracker (*Nucifraga columbiana*). *Animal Cognition*, *14*, 735-744.
- Connor, R. C., Wells, R. S., Mann, J., & Read, A. J. (2000). The bottlenose dolphin: Social relationships in a fission-fusion society. In J. Mann, R. C. Connor, P. L. Tyack, & H. Whitehead (Eds.), *Cetacean societies: Field studies of dolphins and whales* (pp. 91–126). Chicago, IL: University of Chicago Press.

- Douglas-Hamilton, I. & Douglas-Hamilton, O. (1975). *Among the elephants*. London, England: Collins & Harvill.
- Gergely, G. (1994). From self-recognition to theory of mind. In S. T. Parker, R. W. Mitchell & M. L. Boccia (Eds.). *Self-awareness in Animals and Humans* (pp. 51–60). Cambridge, UK: Cambridge University Press.
- Gopnik, A., & Meltzoff, A. N. (1994). Minds, bodies and persons: young children's understanding of the self and others as reflected in imitation and theory of mind research. In S. T. Parker, R. W. Mitchell & M. L. Boccia (Eds.). *Self-awareness in Animals and Humans* (pp. 166–186). Cambridge, England: Cambridge University Press.
- Hare, B., Call, J., & Tomasello, M. (2001). Do chimpanzees know what conspecifics know? *Animal Behaviour*, *61*, 139–151.
- Herman, L. M. (2002). Vocal, social, and self-imitation by bottlenosed dolphins. In C. Nehaniv & K. Dautenhahn (Eds.), *Imitation in animals and artifacts* (pp. 63-108). Cambridge, MA: MIT Press.
- Kaminski, J., Call, J., & Tomasello, M. (2008). Chimpanzees know what others know but not what they believe. *Cognition*, *109*, 224-234.
- McComb, K., Baker, L., & Moss, C. (2006). African elephants show high levels of interest in the skulls and ivory of their own species. *Biology Letters*, *2*, 26-28.
- Moss, C. (1988). *Elephant memories: thirteen years in the life of an elephant family*, (1st ed.). Glasgow, UK: Fontana/Collins.
- Reynolds, J. E., Wells, R. S., & Eide, S. D. (2000). *The bottlenose dolphin: Biology and conservation*. Gainesville, FL: University Press of Florida.

Spinage, C. A. (1994). *Elephants*. London, England: T & A D Poyser.

Whiten, A. (1996). Imitation, pretence, and mindreading: secondary representation in comparative primatology and developmental psychology? In A. E. Russon, K. A. Bard & S. T. Parker (Eds.). *Reaching into Thought: the Minds of the Great Apes* (pp. 300–324). Cambridge, UK: Cambridge University Press.

**Chapter 4: Clark's Nutcrackers (*Nucifraga columbiana*) Flexibly Adapt Caching
Behaviour to a Cooperative Context**

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Abstract

Corvids are able to recognize when their caches are at risk of being stolen by others and have developed strategies to protect these caches from pilferage. For instance, Clark's nutcrackers will suppress the number of caches they make if being observed by a potential thief. Cache protection has most often been studied in social corvids using competitive contexts. Thus, it is unclear whether the Clark's nutcracker, a non-social corvid, will show these cache protection behaviours during a cooperative context. That is, are caching behaviours flexibly adapted to different contexts? In this study, Clark's nutcrackers were given a caching task in which caches made by one individual were reciprocally exchanged for the caches of a partner bird over repeated trials. In this scenario, if caching behaviours can be flexibly deployed, then the birds should recognize the cooperative nature of the task and maintain or increase caching levels over time. However, if cache protection strategies are applied independent of social context and simply in response to cache theft, then cache suppression should occur. In the current experiment, we found that the birds maintained caching throughout the experiment. We report that males increased caching in response to a manipulation in which caches were artificially added, suggesting the birds could adapt to the cooperative nature of the task. Additionally, we show that caching decisions were not solely due to motivational factors, instead showing an additional influence attributed to the behaviour of the partner bird.

Keywords: cache protection; Clark's nutcrackers; complex cognition; cooperation

Why individuals work for the interests of others, at times even against their own benefit, has long been a source of intrigue for evolutionary biologists and comparative psychologists (Axelrod & Hamilton 1981). Such cooperative behaviours are now known to be evolutionarily feasible if they provide inclusive fitness benefits (Brosnan & Bshary 2010; Lehmann & Rousset 2010). However, the conditions in which an individual chooses to act in a cooperative fashion are still unclear (Bshary & Oliveira, 2015). In great apes for instance, although many cooperative acts have been explained by kin selection (Richerson & Boyd, 2005), some instances of cooperation are between non-kin and seem to have more direct and proximate benefits (e.g. alliance formation: Gilby, Wilson, Mohlenhoff, & Pusey, 2009; Watts, 2002; group hunting: Boesch, 1994; Boesch & Boesch 1989; Watts & Mitani 2002; cooperation experiments: Greenberg, Hamann, Warneken & Tomasello, 2010; Hauser, Chen, Chen & Chuang, 2003; Hare and Kwetuenda 2010; Horner, Carter, Suchak & de Waal, 2011; Melis et al., 2011).

The decision-making behind whether to act cooperatively can require complex cognitive abilities, such as cost benefit analysis and social cognition. Acting cooperatively can come with immediate risks, such as in third party conflict resolution (Silk, 1992; Watts, 2002); not acting cooperatively can prevent one from benefiting from joint ventures, such as group hunting (Boesch, 1994), or cause one to be socially ostracized (Boehm 1999). Thus, it would be advantageous for an individual to be capable of judging whether the cooperative act will come at a cost or benefit, and adjust the degree to which one cooperates accordingly (Trivers, 1971). The *social competence hypothesis* (Bshary & Oliveira, 2015; Taborsky & Oliveira, 2012) argues social behaviours evolved to be flexible and that individuals can select from their full range of

behavioural options to adjust to ever changing contexts. However, whether non-human animals have the requisite cognitive skills to allow for this cognitive flexibility is still being questioned (Brosnan, Salwiczek & Bshary, 2010; Stevens & Hauser, 2004).

Complex cognition has traditionally been viewed as the result of the evolutionary demands of living in large, complex social groups and hence the reason for primates', once thought, unique intelligence (Humphrey, 1976). Indeed, primates have been shown capable of some of the cognitive abilities thought to underlie cooperation, such as adjusting to cost/benefit changes (Marsh & MacDonald, 2012), or responding to the mental states of others (e.g., Flombaum & Santos, 2005; Hare, Call & Tomasello, 2001). Thus, primates have been the primary source of research examining psychological aspects of non-human animal cooperation. Indeed, some evidence suggests chimpanzees can be flexible in how they cooperate if allowed to negotiate with a partner (Melis, Hare & Tomasello, 2009) and this cooperation is not always driven by kin selection (Greenberg et al. 2010; Hare & Kwetuenda 2010; Horner et al. 2011; Melis et al. 2011). Therefore, prompting an individual to consider and respond to the needs of potential partners could be an important precursor for successful cooperation (Burkart et al. 2009; Trivers, 1971; de Waal & Suchak 2010; Eisenberg & Mussen, 1989; Silk 2007).

Corvids are increasingly reported to be clever problem solvers. Research investigating relatively social corvids has shown their cognitive abilities rival those of primates, especially in the domain of social cognition (Emery & Clayton, 2004, 2009). As expressed by their food caching (i.e., hiding food for later use) behaviours, social corvids seem to consider the visual perspective of other birds when hiding caches (Bugnyar, 2011; Clayton, Dally & Emery, 2007; Dally, Emery & Clayton, 2004), infer

the intent of other birds to steal their caches (Bugnyar & Heinrich, 2006; Emery, Dally & Clayton, 2004) and use their own experience as thieves to anticipate the need to protect their caches (Emery & Clayton, 2001). Additionally, social corvids have been found to make cooperative decisions in both natural ecological (cooperative breeding: Woolfenden & Fitzpatrick, 1996; reciprocal agonistic support: Fraser & Bugnyar, 2011; food sharing: de Kort, Emery & Clayton, 2006; Scheid, Schmidt & Noë, 2008; von Bayern, de Kort, Clayton & Emery, 2007) and laboratory conditions (Scheid & Noë, 2010; Schwab, Swoboda, Kotrschal & Bugnyar, 2012; Stephens, McLinn & Stevens, 2002). Thus, the work with social corvids has provided additional support for theories suggesting social living is important for the evolution of complex cognition. However, research examining relatively non-social corvids suggests these birds may share the abilities of their social counterparts, including inferring intentions of potential thieves (Clary & Kelly, 2011; Shaw & Clayton, 2012) and sensitivity to the mental states of others (Clary & Kelly, 2013; Ostojic, Shaw, Cheke & Clayton, 2013). Therefore, social living is unlikely to be solely responsible for the complex cognitive abilities of corvids. Whether social living is important for cooperative behaviours in particular however, has not been well studied.

In this study we developed a novel procedure to examine whether Clark's nutcrackers (*Nucifraga columbiana*), which are relatively non-social compared to other corvids, use a competitive or cooperative caching strategy if given a cooperative caching task. When examined in a competitive context, nutcrackers suppress caching when observed by a conspecific (Chapter 2; Clary & Kelly, 2011; Tomback, 1998), whereas relatively more social Western scrub-jays have been found to increase caching (Emery et al., 2004). Clary and Kelly (2011) suggested that caching behaviours might be influenced

by sociality with less social species viewing caching situations as more competitive than social species, and less prone to accept risk to their caches. However, caching paradigms used to date involve competitive situations. Hence, in this study we examined whether caching behaviours can be flexibly adapted to a cooperative context, and in doing so, further evaluate the cognitive capabilities of non-social corvids. To do so, nutcrackers were given a caching task in which birds made caches that were only recovered by a partner, and in turn they only received their partner's caches. The birds experienced this situation over repeated trials, and thus had the opportunity to learn the partner's caching patterns. As such, the structure resembles, though is not identical, to a continuous, iterated prisoner's dilemma (Doebeli & Hauert, 2005; Raihany & Bshary, 2011), as a bird must balance the energetic cost of caching with the benefits from receiving caches, with the greatest potential payoff coming from exploiting a cooperative partner.

In the classic single-game format of the prisoner's dilemma, defection is the evolutionary stable strategy, as the payoffs are highest when exploiting a cooperative partner and lowest if cooperating without a reciprocating partner. However, cooperation is more likely to be maintained (though not guaranteed) as a beneficial strategy when the game is repeated as it allows for cooperation and defection to be reciprocated (Axelrod & Hamilton, 1981; Doebeli & Hauert, 2005). By allowing for repetition in our novel task, we attempted to provide conditions favourable for cooperation. Therefore, if the nutcrackers flexibly adjust their caching strategies they should mutually cooperate during the task by continuing to cache for the benefit of the partner bird. Alternatively, if the nutcrackers' caching behaviour is constrained by species-specific tendencies (e.g., always suppress caching when observed), then a decrease in caching over time would be

expected, despite each bird gaining reinforcement by recovering the partner's caches.

Methods

Subjects

Fourteen sexually mature, wild-caught Clark's nutcrackers (7 male, 7 female) were used in this experiment. As in the competitive caching task previously used with nutcrackers (Clary & Kelly, 2011), each bird was tested with an opposite sex partner for the duration of the experiment. The nutcrackers were of unknown age, but had been in the laboratory for a minimum of 7 years. The birds had participated in a pilot study (unpublished data) in which they cached in the presence of a conspecific, but none had experienced cache theft in an experimental context. The colony rooms were maintained at a stable temperature of 22°C and a 12 hr light cycle, with light onset at 0700. Birds were housed in individual cages (48 cm length x 48 cm width x 73 cm height) with multiple perches for the duration of the experiment with water and grit provided *ad libitum*. All birds were fed *ad libitum* except on test days (see procedure). Nutcrackers were fed a diet consisting of turkey starter, parrot pellets, sunflower seeds, mealworms, peanuts, pine nuts, and a vitamin supplement. All animal care procedures were approved by the local animal care committee (approval #F10-029) and were in accordance with the guidelines of the Canadian Council on Animal Care.

Apparatus

Birds were tested in their home cages, which were transported to an experimental room. The cages were placed on a table (121 cm long x 60 cm wide) and positioned so, when perched, the birds faced one another. The table was surrounded by white curtains (200 cm long x 175 cm wide) to provide a uniform viewing environment. An ice cube

tray filled with sand was provided to each bird to allow caching (tray consisted of 26 wells arranged in a 13 x 2 matrix; overall dimensions: 49.5 cm long x 11 cm wide). A combination of Mega Building Blocks™ affixed to the trays uniquely identified each bird's caching tray, a procedure commonly (and successfully) used to facilitate tray discrimination (e.g., Clary & Kelly, 2011; Emery et al., 2004). All trials were recorded using four EverFocus 1/3" color digital cameras and the software package BiObserve.

Procedure

Food deprivation. All birds were food deprived 24 hours prior to participating in a weekly trial. A weekly trial consisted of a *Caching Session* during the first day and a *Retrieve Session* during the second day. During the *Caching Session* birds had the opportunity to eat and/or cache 50 pine nuts. After the *Caching Session*, birds were supplemented with a restricted amount of regular feed to maintain the bird at a healthy weight. After completing the *Retrieve Session*, birds were returned to an *ad libitum* diet until the next week's trial. Birds were weighed daily to ensure a healthy weight was maintained throughout the experiment and to measure both motivation to eat when outside the weekly trials and motivation to cache during each *Caching Session*.

Baseline trials. Each bird experienced six baseline trials. Before the trial, both birds of a pair were transported to the experiment room. During the *Caching Session*, an experimenter gave the first bird of the pair its visually unique caching tray, positioned horizontally relative to the partner bird's viewing position, and a dish containing 50 pine nuts. The first bird was allowed to eat and cache the pine nuts for 45 min, after which, the tray and pine nut dish was removed from the bird's cage and placed visibly between the two cages, out of reach of both birds. The second bird of the pair was then given its

visually unique caching tray and dish of 50 pine nuts and allowed to eat and cache for 45 min. The bird that cached first was alternated on a weekly basis. After the *Caching Session* the birds were returned to the colony room and the number of pine nuts eaten, the number of caches made in the tray, and the number of caches made external to the tray, for each bird, was documented.

The next day, the birds were returned to the experiment room to participate in the *Retrieval Session*. During the *Retrieval Session*, both birds were provided with their original caching tray and allowed to recover their cached food (i.e., both birds recovered their caches at the same time). *Retrieval Sessions* lasted one hour, after which, the birds were returned to the colony room and the number of remaining caches documented. Nutcrackers have previously been shown to remember caches accurately after 285 days (Balda & Kamil, 1992); therefore, if caches remained in the tray, then subsequent *Retrieval Sessions* were conducted on the following day until all caches were recovered. This was done to prevent memories of previously made and unrecovered caches from interfering with the caches made during the next *Caching Session*.

Cache sharing. Each bird experienced 12 cache sharing trials, starting the week immediately following the completion of baseline trials. Procedures for these trials were identical to those of the baseline trials, with the exception that during the *Retrieve Session* instead of the birds receiving their own caching tray, the birds received their partner's caching tray.

Cache addition. Each bird experienced six cache addition trials following completion of all cache sharing trials. Procedures were identical to the cache sharing condition except that after the *Caching Session*, the experimenter added caches to the

trays so that each individual received twice the maximum number of caches received on a single trial from the partner during cache sharing. This procedure was conducted to examine whether an exaggerated cooperative response would be elicited from the birds if it seemed that the partner had become more generous.

Statistical Analysis

The data were blocked so as to compare the average of the six Baseline trials, the first six Cache Sharing trials, the second six Cache Sharing trials, and the six Cache Addition trials. As the caching behaviours were highly variable according to individual and sex, the variables (number of caches remaining in the tray, number of external caches, number of pine nuts eaten, number of caching events, and weight of the bird) were standardized by computing them as a proportion of the values measured in the Baseline trials. Caching events (herein referred to simply as ‘events’ to disambiguate from caches remaining in the tray) were scored from the videos and defined as any instance when the bird placed a pine nut in the sand of the tray, and therefore included all re-caches (i.e., repeated placements of a single pine nut), serving as a more general measure of caching activity. Latency from the time the birds jumped down to the bottom of the cage to when they made contact with the tray was also scored from the recorded trials. Due to a program error, some trials were not recorded properly and could not be scored (Baseline: 4/84; Cache Sharing 1: 2/84; Cache Sharing 2: 17/84; Cache Addition: 2/84). This imbalance was accounted for with our use of a mixed-effect modeling technique (described below), which is robust to missing values (Baraldi & Enders, 2010).

To assess if any of the variables changed over different blocks or trials of the experiment, we used linear mixed-effects models with block/trial and sex inputted as

fixed effects along with their interaction, and subject inputted as a random effect. We also created linear mixed-effects models based on the Cache Sharing trials alone to assess whether the birds' caching was influenced by social factors or by motivational factors. This model included weight of the focal bird, the number of caches made by the partner, and the number of caching events of the partner inputted as fixed effects, and subject inputted as a random effect. We excluded the first trial of the Cache Sharing block as the birds would not have had a chance to learn the procedures by this point, and replaced this trial with the first Cache Addition trial. Since we alternated which bird cached first, one bird of the pair on any given trial would not have the opportunity to base their caching on the partner's caching, unless relying on what they experienced during the previous week's trial. To account for this we computed a running mean of two trials for the number of caches made by the focal bird, so that each data point represented the average of when a bird went first and second. For all analyses parameter estimation was achieved using residual maximum likelihood and degrees of freedom were estimated using Satterthwaite approximation. Analyses were performed in R version 3.1.2 using the *lme4* (Bates, Maechler, Bolker & Walker, 2014) and *lmerTest* packages (Kuznetsova, Brockhoff & Christensen, 2015). Results from the mixed-effects model were comparable to results produced from more traditional multivariate techniques.

Results

Changes over Blocks/Trials

Caching. When examining the proportion of baseline caches made in the tray(s), there was an interaction between block and sex ($F_{(3, 316)} = 2.833, p = 0.038$). There was an effect of sex only during the Cache Addition block ($t_{(23.62)} = 2.227, p = 0.036, d = 0.59$).

This was due to an increase in proportion of caches made by the males during the Cache Addition block (Baseline: $t_{(316)} = -2.889$, $p = 0.004$, $d = 1.09$; Cache Sharing 1: $t_{(316)} = -1.741$, $p = 0.083$, $d = 0.66$; Cache Sharing 2: $t_{(316)} = -1.886$, $p = 0.060$, $d = 0.71$; Figure 1), whereas no detectable statistical change was observed for females during Cache Addition relative to other blocks (Baseline: $t_{(316)} = 0.695$, $p = 0.488$; Cache Sharing 1: $t_{(316)} = 1.194$, $p = 0.233$; Cache Sharing 2: $t_{(316)} = 1.556$, $p = 0.121$). The change in proportion of caches made eliminated the tendency for females to make more absolute number of caches than males (see Figure 2).

A similar interaction between block and sex ($F_{(3, 291)} = 9.110$, $p < 0.001$) was observed by analyzing the proportion of baseline events (i.e., combined caches and recaches). This was driven by an increase in proportion of events made by males (Cache Sharing 1 – Cache Sharing 2: $t_{(291)} = 2.688$, $p = 0.008$, $d = 1.01$; Cache Sharing 2 – Cache Addition: $t_{(291)} = 2.800$, $p = 0.005$, $d = 1.06$; Figure 3), and a decrease back to baseline by females (Cache Sharing 2 – Cache Addition: $t_{(291)} = 1.872$, $p = 0.062$, $d = 0.71$). For the proportion of baseline external caches we found no effect of block ($F_{(3, 316)} = 0.207$, $p = 0.892$), sex ($F_{(1, 12)} = 0.086$, $p = 0.775$), nor a block by sex interaction ($F_{(3, 316)} = 1.781$, $p = 0.151$).

Latency. To ensure the birds understood the trays were switched during the Cache Sharing trials we examined their latency to approach the tray. An increase in latency to approach the tray was found on the first Cache Sharing trial compared to the last Baseline trial ($t_{(60)} = 2.978$, $p = 0.004$, $d = 0.80$; Figure 4) suggesting the birds recognized a difference in trays. Latency quickly decreased during subsequent trials suggesting the birds quickly came to expect the new tray.

Eating/Weight. There was a main effect of block on the number of pine nuts eaten ($F_{(3, 316)} = 12.445, p < 0.001$). Both males and females ate less pine nuts during trials of the Cache Addition block compared to all other blocks (Baseline: $t_{(319)} = 4.819, p < 0.001, d = 1.29$; Cache Sharing 1: $t_{(319)} = 5.506, p < 0.001, d = 1.47$; Cache Sharing 2: $t_{(319)} = 4.476, p < 0.001, d = 1.20$; Figure 5).

An interaction of block and sex was found for the proportion of the birds' weight during baseline ($F_{(3, 316)} = 8.696, p < 0.001$). This was due to an effect of sex found only during the Cache Addition block ($t_{(26.93)} = -4.100, p < 0.001, d = 1.10$), as males showed a reduction in weight during the Cache Addition block compared to all other blocks (Baseline: $t_{(316)} = 3.631, p < 0.001, d = 1.37$; Cache Sharing 1: $t_{(316)} = 5.878, p < 0.001, d = 2.22$; Cache Sharing 2: $t_{(316)} = 4.275, p < 0.001, d = 1.62$; Figure 6), whereas females showed an increase in weight during Cache Addition relative to Baseline ($t_{(316)} = -2.498, p = 0.013, d = 0.94$), though this weight was not different from the Cache Sharing blocks (Cache Sharing 1: $t_{(316)} = -0.340, p = 0.734$; Cache Sharing 2: $t_{(316)} = -0.789, p = 0.431$).

Predictors of Caching Behaviour

Males. When examining proportion of Baseline caches there was no effect of the partner's caches ($R = -0.147, F_{(1, 75.05)} = 3.390, p = 0.070$) nor weight of the focal bird ($R = -2.256, F_{(1, 79.97)} = 0.394, p = 0.532$), but there was a marginal positive effect of the partner's events ($R = 0.151, F_{(1, 77.72)} = 3.871, p = 0.053$). When examining proportion of Baseline events, there was a positive effect of the partner's events ($R = 0.606, F_{(1, 78.94)} = 8.495, p = 0.005$) and a negative effect of weight of the focal bird ($R = -33.173, F_{(1, 78.97)} = 11.810, p = 0.001$), but no effect of the partner's tray caches ($R = -0.058, F_{(1, 75.35)} = 0.0706, p = 0.791$).

Females. When examining proportion of Baseline caches, we found no effect of the partner's tray caches ($R = -0.088$, $F_{(1, 35.87)} = 0.282$, $p = 0.600$), the partner's events ($R = -0.043$, $F_{(1, 47.70)} = 0.351$, $p = 0.557$), nor the weight of the focal bird ($R = 11.378$, $F_{(1, 52.67)} = 2.816$, $p = 0.100$). When examining proportion of Baseline events, there was a positive effect of both the partner's tray caches ($R = 0.288$, $F_{(1, 53.05)} = 4.866$, $p = 0.032$) and the partner's events ($R = 0.122$, $F_{(1, 69.15)} = 4.835$, $p = 0.031$), but no effect of the focal bird's weight ($R = 6.309$, $F_{(1, 71.34)} = 1.476$, $p = 0.228$).

Discussion

The birds maintained caching levels throughout the Cache Sharing trials, despite recognizing the trays were switched, showing no detectable change in strategy: neither an increase in caching indicative of overt cooperation, nor a decrease in caching indicative of competition. Though this finding may reflect the birds' baseline motivational drive to cache (Clayton & Dickinson, 1999), it is in contrast to previous findings that nutcrackers suppress their caching over time in response to witnessing cache theft in a competitive context (Clary & Kelly, 2011; Chapter 2). When the birds experienced artificially exaggerated cooperation during Cache Addition, the males seemed to respond cooperatively, whereas the females maintained baseline levels of caching behaviours. Interestingly, the change in caching reduced the inequity in absolute number of pine nuts exchanged between the partners. The increase in caching by males during the Cache Addition block is peculiar in that these caches only benefit the other individual. By this point in the experiment, the birds would have had ample opportunity to learn they are never provided with an opportunity to recover their own caches, yet the males responded to receiving more caches by caching more themselves and incurring additional costs by

eating less. Therefore, if non-social corvids, like nutcrackers, do have an inherent tendency to cache competitively as suggested by Clary and Kelly (2011), then this tendency was easily over-ridden to fit the cooperation-biased structure and non-ecologically relevant cache sharing aspects of this caching task.

Another interpretation could be that the nutcrackers' caching was already suppressed during baseline, despite extended experience learning their caches were always returned in an intact state from the baseline trials and the earlier conducted pilot study. This learning may have interfered with detecting further cache suppression. Looking at the absolute caching values in comparison with our previous research (Clary & Kelly, 2011) indicates this may have been the case, though mainly for the males. Under this interpretation, the males' responses during Cache Addition would be an alleviation of existing cache suppression. Regardless of interpretation, the results indicate the males adjusted their caching decisions based on the experimental context.

There were also changes in motivational variables during the Cache Addition block, as the increase in caching by males corresponded with a decrease in weight and pine nuts eaten during the *Cache Session*, whereas females, along with maintaining caching behaviours, maintained their weight and showed a reduction in pine nuts eaten. Thus, it seems the birds anticipated receiving caches during the *Retrieve Session* of Cache Addition trials. This was shown by the birds eating less during the *Cache Session*, as well as by the males no longer compensating for the weekly food deprivation by consuming more food during the five days between weekly trials. Therefore, although it is possible the birds did not understand that trials would be repeated, these results suggest the birds came to expect receiving food in future trials or sessions.

As predictors of caching behaviour, a combination of motivational and social factors were found to influence the birds' caching decisions, with both weight of the bird, but more consistently, the events of the partner explaining variance in the focal bird's caching behaviours. Therefore, the birds seemed to match the overall caching activity (caching and recaching) of the other bird. These results were likely driven by recaches possibly indicating the birds were either still engaging in cache protection or attempting to extract more cooperation from the partner by appearing more cooperative. Either interpretation suggests the birds were reluctant cooperators. Importantly however, this shows the birds were not responding solely based on motivational factors, but also attending to the behaviour of their partner, consistent with previous research indicating that nutcrackers use observational spatial memory to track the caches of others (Bednekoff & Balda, 1996).

From an ecological perspective, considering there was an initial investment that is only recouped through a similar investment by the partner, the nutcrackers' behaviour could be labeled as reciprocity (Raihani & Bshary, 2011). That cooperation emerged in this experimental structure, with payoffs resembling a prisoner's dilemma, is interesting as past research has found that animals often converge on mutual defection in these tasks (Clements & Stephens, 1995; Flood, Lendenmann & Rappoport, 1983; Hall, 2003). However, our prisoner's dilemma structure contained features that game theoretical models predict to facilitate cooperation: iteration and alternation (Doebeli & Hauert, 2005). Indeed, when conditions and payoffs are carefully constructed to favor cooperation, experimental contexts find cooperation in iterated prisoner's dilemma tasks

(Pinto, Oates, Grutter & Bshary, 2011; Rutte & Taborsky, 2007; St. Pierre, Larose & Dubois, 2009; Viana, Gordo, Sucena & Moita, 2010)

Another interpretation could be that the increase in caching was due to courtship behaviour, accounting for the more pronounced response of the males, and would not require the birds to understand the cooperative aspects of the task (though still cooperative in an ecological sense: Stevens & Gilby, 2004). For many species, males provision females to facilitate pair bonding or mating attempts (Lewis & South, 2012). Though both males and females continued to cache at baseline levels throughout the Cache Sharing trials instead of suppressing their caching over time (as previously found for this species), it is curious that only males responded so strongly to Cache Addition. It could be that males were advertising their quality to the females by caching more and eating less. However, if this behaviour was related to courtship it is odd that it only manifested during the Cache Addition block (18 weeks after experiment onset), during which the males also benefited by receiving extra caches. Furthermore, courtship displays were not observed during the trials of the current study, nor among the male-female pairs used by Clary and Kelly (2011), which resulted in cache suppression.

Although we could describe the behaviour of the nutcrackers as cooperative from an ecological perspective, this need not be the case psychologically. The results could be due to an associative mechanism. By adding caches during Cache Addition, it could be argued that positive associations with the environment and the behaviours engaged in within that environment are enhanced. If receiving caches acts as a positive reinforcer for caching behaviour, then it would be expected that the frequency of caching behaviours would increase. Indeed, the number of events increased over trials, although only for the

males. That females made slightly more caches than males, and thus experienced a net cache loss during the exchange in Cache Sharing, could explain why females did not show an increase in tray caches or events before Cache Addition. However, it is unclear why females would be resistant to this associative mechanism when it should be strongest (i.e., after Cache Addition). Additionally, the ‘predictors of caching behaviour’ analyses revealed that caching decisions were not largely driven by the caches received (reinforcement based), but instead influenced mostly by the activity level of the partner. Similarly, previous research using greater trial numbers has found no positive feedback due to cache recovery (Chapter 2; Thom & Clayton, 2014), despite corvids typically learning rapidly in caching tasks (trials 1-3: e.g., Clary & Kelly, 2011; Correia, Dickinson & Clayton, 2007; Raby, Alexis, Dickinson & Clayton, 2007). Furthermore, when caching behaviour has been explicitly tested with respect to associative learning, nutcrackers did not alter their caching behaviour when cache loss was paired with an inanimate object (Clary & Kelly, 2011).

Independent of which explanations are invoked, this type of response to unexpected caches could provide a mechanism for offsetting the high pilferage rates in the wild as noted by Vander Wall and Jenkins (2003). Ostensibly, caching is a disadvantageous strategy prone to being infiltrated by cheating strategies; however, the authors showed that caching could be maintained as an evolutionarily advantageous strategy through reciprocity of pilferage, though this reciprocity was based on exploitation, rather than altruism. If individuals respond to finding unexpected caches by increasing their own caching, as shown here, it would offset the costs of the theft victim by making it more likely they will reciprocally pilfer the caches of others in the future.

Furthermore, if natural caching exchanges resemble cooperation in that they follow the payoffs of a prisoner's dilemma, then we may expect decisions on where to cache to be influenced by similar factors, particularly the spatial distribution and stability of neighbouring individuals allowing for iteration and choice of partners.

Our novel task provides a variety of strengths over previous tasks devised to investigate cooperative behaviours in non-human animals. First, due to the caching context, the food is not visible at the time of cooperation. During studies with primates, visible food has been found to inhibit prosocial choices (Bullinger, Melis & Tomasello, 2011; Jensen, Hare, Call & Tomasello, 2006; Silk et al. 2005; Vonk et al. 2008). Second, researchers have expressed concern over some species' tendency to discount the future in favor of current motivational needs (Stephens et al., 2002). Using Clark's nutcrackers, a caching species that relies on long-term spatial memory to recover food stores (see Kamil & Balda, 1990 for a review), minimizes this concern as they likely make caching decisions to satisfy future, rather than immediate, motivational needs (as is the case for Western scrub jays: Correia et al., 2007; Raby et al., 2007; Thom & Clayton, 2014). Third, during experiments with greater physical distance between animals, null results for cooperation have been found (Jensen et al., 2006; Vonk et al., 2008). During our experiment there was small physical separation between the two birds, which has been argued to facilitate cooperation (Horner, et al., 2011).

From a proximate perspective, it seems the nutcrackers were able to adjust their caching to accommodate a cooperative experimental context – as long as cooperation from the partner was established and maintained (see also St. Pierre, Larose & Dubois, 2009), as males first required cache addition before increasing their own caching. In this

sense, the males were willing to work against their own interests, only if they could accrue some selfish benefit. From an ultimate perspective, this research suggests that high levels of sociality (group living) are not required for the development of flexible social cognition, nor the ability to cooperate, and consistent with observations that social learning mechanisms are not unique to social species (Heyes, 2012). However, at this point we cannot conclude definitively whether the males understood the cooperative aspects of the task, only that their caching behaviours exhibit flexibility to accommodate atypical contexts. Conversely, game theoretical models predict that smaller group sizes favour the development of cooperation (Doebeli & Hauert, 2005). It may then be that the conditions for successful cooperation favour moderately social species, especially those with the cognitive abilities to track the more dynamic social aspects of cooperation, such as individual characteristics (e.g., dominance, reputation) and intentions. Here, using a novel task, we show that a relatively non-social species, which typically suppresses caching in the presence of others (Clary & Kelly, 2011) and prefers to make and retrieve caches solitarily (Tomback, 1998), can show flexibility in their caching strategy according to changing social contexts. This behavioural flexibility is consistent with the social competence hypothesis that suggests phenotypic plasticity allows animals to cope with their social world and predicts animals to optimize their social choices to account for changing contextual factors (Bshary & Oliveira, 2015). Theories of group living have relied on the results of social species to make assumptions about the nature of complex cognitive abilities, our study adds to this discussion by documenting the abilities of a non-social species. The novel procedure described here generates exciting new questions regarding the flexibility of corvid caching and further testing is certainly required to

evaluate how animals acquire the ability to reason about social partners, to cooperate based on those judgments, and to isolate the mechanisms responsible for cooperation.

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References

- Axelrod, R., & Hamilton, W.D. (1981). The evolution of cooperation. *Science*, *211*, 1390–1396.
- Balda, R. P., & Kamil, A. C. (1992). Long-term spatial memory in Clark's nutcracker, *Nucifraga columbiana*. *Animal Behaviour*, *44*, 761–769.
- Baraldi, A. N., & Enders, C. K. (2010). An introduction to modern missing data analyses. *Journal of School Psychology*, *48*, 5-37.
- Bates, D., Maechler, M., Bolker, B., & Walker S. (2014). *_lme4: Linear mixed-effects models using Eigen and S4_*. R package version 1.1-7, <URL: <http://CRAN.R-project.org/package=lme4>>.
- Bednekoff, P. A., & Balda, R. P. (1996). Observational spatial memory in Clark's nutcrackers and Mexican jays. *Animal Behaviour*, *52*, 833–839. Retrieved from <http://linkinghub.elsevier.com/retrieve/pii/S0003347296902286>
- Boehm, C. (1999). *Hierarchy in the forest: the evolution of egalitarian behavior*. Cambridge, MA: Harvard University Press.
- Boesch, C. (1994). Cooperative hunting in wild chimpanzees. *Animal Behaviour*, *48*, 653–667.
- Boesch, C., & Boesch, H. (1989). Hunting behavior of wild chimpanzees in the Tai National Park. *American Journal of Physical Anthropology*, *78*, 547–573.
- Brosnan, S. F., & Bshary, R. (2010). Cooperation and deception: from evolution to mechanisms. *Philosophical Transactions of the Royal Society: Biological Sciences*, *365*, 2593–2598.

- Brosnan, S. F., Salwiczek, L., & Bshary, R. (2010). The interplay of cognition and cooperation. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*, 2699–2710.
- Bshary, R., & Oliveira, R. F. (2015). Cooperation in animals: toward a game theory within the framework of social competence. *Current Opinion in Behavioral Sciences*, *3*, 31-37.
- Bugnyar, T. (2011). Knower-guesser differentiation in ravens: Others' viewpoints matter. *Proceedings of the Royal Society: Biological Sciences*, *278*, 634-640.
- Bugnyar, T., & Heinrich, B. (2006). Pilfering ravens, *Corvus corax*, adjust their behavior to social context and identity of competitors. *Animal Cognition*, *9*, 369-376.
- Bullinger, A. F., Melis, A. P., & Tomasello, M. (2011). Chimpanzees, *Pan troglodytes*, prefer individual over collaborative strategies toward goals. *Animal Behaviour*, *82*, 1135–1141.
- Burkart, J. M., Hrdy, S. B., & van Schaik, C. P. (2009). Cooperative breeding and human cognitive evolution. *Evolutionary Anthropology*, *18*, 175–186.
- Clary, D., & Kelly, D. M. (2011). Cache protection strategies of a non-social food-caching corvid, Clark's nutcracker (*Nucifraga columbiana*). *Animal Cognition*, *14*, 735-744.
- Clary, D., & Kelly, D. M. (2013). Are Clark's nutcrackers (*Nucifraga columbiana*) able to discriminate knowledge states of human experimenters during an object-choice task? *Evolutionary Psychology*, *11*, 628-646.

- 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., & Dickinson, A. (1999). Motivational control of caching behaviour in the scrub jay, *Aphelocoma coerulescens*. *Animal Behaviour*, *57*(2), 435-444.
- Clements, K. C., & Stephens, D. W. (1995). Testing models of non-kin cooperation: mutualism and the prisoner's dilemma. *Animal Behaviour*, *50*, 527-535.
- 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.
- Dally, J. M., Emery, N. J., & Clayton, N. S. (2004). Cache protection strategies in western scrub-jays (*Aphelocoma californica*): Hiding food in the shade. *Proceedings of the Royal Society: Biological Sciences*, *271*, 387-390.
- 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 Waal, F. B. M., & Suchak, M. (2010). Prosocial primates: selfish and unselfish motivations. *Philosophical Transactions of the Royal Society: Biological Sciences*, *365*, 2711-2722.
- Doebeli, M., & Hauert, C. (2005). Models of cooperation based on the Prisoner's Dilemma and the Snowdrift game. *Ecology Letters*, *8*, 748-766.
- Eisenberg, N., & Mussen, P. H. (1989). The roots of prosocial behavior in children. Cambridge, UK: Cambridge University Press.

Emery, N. J., Dally, J. M., & Clayton, N. S. (2004). Western scrub-jays (*Aphelocoma californica*) use cognitive strategies to protect their caches from thieving conspecifics. *Animal Cognition*, 7, 37-43.

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. (2004). The mentality of crows: Convergent evolution of intelligence in corvids and apes. *Science*, 306, 1903-1907.

Emery, N. J., & Clayton, N. S. (2009). Comparative Social Cognition. *Annual Review of Psychology*, 60, 87-113.

Flombaum, J., & Santos, L. (2005). Rhesus monkeys attribute perceptions to others. *Current Biology*, 15, 447-452.

Flood, M., Lendenmann, K., & Rappoport, A. (1983). 2x2 Games played by rats: different delays of reinforcement as payoffs. *Behavioral Science*, 28, 65-78.

Fraser, O. N., & Bugnyar, T. (2011). Reciprocity of agonistic support in ravens. *Animal Behaviour*, 83, 171-177.

Gilby, I. C., Wilson, M. W., Mohlenhoff, K. A., & Pusey, A. E. (2009). The function of coalitionary aggression among wild chimpanzees. *American Journal of Physical Anthropology*. (Suppl. 48), 133.

Greenberg, J. R., Hamann, K., Warneken, F., & Tomasello, M. (2010). Chimpanzee helping in collaborative and noncollaborative contexts. *Animal Behaviour*, 80, 873-880.

Hall, S. S. (2003). Transitions between cooperative and non-cooperative responding in the pigeon's dilemma. *Behavioural Processes*, 60, 199-208.

- Hare, B., Call, J., & Tomasello, M. (2001). Do chimpanzees know what conspecifics know? *Animal Behaviour*, *61*, 139-151.
- Hare, B. & Kwetuenda, S. (2010). Bonobos voluntarily share their own food with others. *Current Biology*, *20*, 230–231.
- Hauser, M. D., Chen, K. M., Chen, F., & Chuang, E. (2003). Give unto others: genetically unrelated cotton-top tamarin monkeys preferentially give food to those who altruistically give food back. *Proceedings of the Royal Society B: Biological Sciences*, *270*, 2363-2370.
- Heyes, C. (2012). What's social about social learning? *Journal of Comparative Psychology*, *126*, 129-202.
- Horner, V., Carter, J. D., Suchak, M., & de Waal, F. B. M. (2011). Spontaneous prosocial choice by chimpanzees. *Proceedings of the National Academy of Sciences*, *108*, 13847–13851.
- Humphrey, N. K. (1976). The social function of intellect. In P. P. G. Bateson & R. A. Hinde (Eds.) *Growing points in ethology* (pp. 303-317). Cambridge, UK: Cambridge University Press.
- Jensen, K., Hare, B., Call, J., & Tomasello, M. (2006). What's in it for me? Self-regard precludes altruism and spite in chimpanzees. *Proceedings of the Royal Society B: Biological Sciences*, *273*, 1013–1021.
- Kamil, A. C., & Balda, R. P. (1990). Spatial memory in seed-caching corvids. In G. H. Bower (Ed.), *The psychology of learning and motivation* (pp. 1-25). New York, NY: Academic Press.

- Kuznetsova, A., Brockhoff, P. B., & Christensen, R. H. B. (2015). lmerTest: Tests in Linear Mixed Effects Models. R package version 2.0-25. <http://CRAN.R-project.org/package=lmerTest>
- Lehmann, L., & Rousset, F. (2010). How life history and demography promote or inhibit the evolution of helping behaviours. *Philosophical Transactions of the Royal Society: Biological Sciences*, *365*, 2599–2617.
- Lewis, S., & South, A. (2012). The evolution of animal nuptial gifts. *Advances in the Study of Behavior*, *44*, 53-97.
- Marsh, H., & MacDonald, S. (2012). Orangutans (*Pongo abelii*) “play the odds”: information-seeking strategies in relation to cost, risk, and benefit. *Journal of Comparative Psychology*, *126*, 263-278.
- Melis, A. P., Hare, B., & Tomasello, M. (2009). Chimpanzees coordinate in a negotiation game. *Evolution and Human Behavior*, *30*, 381-392.
- Melis, A. P., Warneken, F., Jensen, K., Schneider, A., Call, J., & Tomasello, M. (2011). Chimpanzees help conspecifics obtain food and non-food items. *Proceedings of the Royal Society: Biological Sciences*, *278*, 1405–1413.
- Ostojić, L., Shaw, R. C., Cheke, L. G., & Clayton, N. S. (2013). Evidence suggesting that desire-state attribution may govern food sharing in Eurasian jays. *Proceedings of the National Academy of Sciences*, *110*, 4123-4128.
- Pinto, A., Oates, J., Grutter, A., & Bshary, R. (2011). Cleaner wrasses *Labroides dimidiatus* are more cooperative in the presence of an audience. *Current Biology*, *21*, 1140-1144.

- Raby, C. R., Alexis, D. M., Dickinson, A., & Clayton, N. S. (2007). Planning for the future by Western Scrub-Jays. *Nature*, *445*, 919–921.
- Raihani, N. J., & Bshary, R. (2011). Resolving the iterated prisoner's dilemma: theory and reality. *Journal of Evolutionary Biology*, *24*, 1628-1639.
- Richerson, P. J., & Boyd, R. (2005). *Not by genes alone*. Chicago, IL: University of Chicago Press.
- Rutte, C., & Taborsky, M. (2007). Generalized reciprocity in rats. *PLoS Biology*, *5*, e196.
- Scheid, C., & Noë, R. (2010). The performance of rooks in a cooperative task depends on their temperament. *Animal Cognition*, *13*, 545-553.
- Scheid, C., Schmidt, J., & Noë, R. (2008). Distinct patterns of food offering and co-feeding in rooks. *Animal Behaviour*, *76*, 1701-1707.
- Schwab, C., Swoboda, R., Kotrschal, K., & Bugnyar, T. (2012). Recipients affect prosocial and altruistic choices in jackdaws, *Corvus monedula*. *PLoS one*, *7*, e34922.
- Shaw, R. C., & Clayton, N.S. (2012). Eurasian jays, *Garrulus glandarius*, flexibly switch caching and pilfering tactics in response to social context. *Animal Behaviour*, *84*, 1191-1200.
- Silk, J. B. (1992). The patterning of intervention among male bonnet macaques: reciprocity, revenge, and loyalty. *Current Anthropology*, *33*, 318e325.
- Silk, J. B. (2007). Empathy, sympathy, and prosocial preferences in primates. In R. I. M. Dunbar & L. Barrett (Eds.) *Oxford handbook of evolutionary psychology* (pp. 115–126). New York, NY: Oxford University Press.

- Silk, J. B., Brosnan, S. F., Vonk, J., Henrich, J., Povinelli, D. J., Richardson, A. S., Lambeth, S. P., Mascaró, J., & Schapiro, S. J. (2005). Chimpanzees are indifferent to the welfare of unrelated group members. *Nature*, *437*, 1357–1359.
- Stephens, D. W., McLinn, C. M., & Stevens, J. R. (2002). Discounting and reciprocity in an iterated prisoner's dilemma. *Science*, *298*, 2216–2218.
- Stevens, J. R., & Gilby, I. C. (2004). A conceptual framework for nonkin food sharing: Timing and currency of benefits. *Animal Behaviour*, *67*(4), 603–614.
doi:10.1016/j.anbehav.2003.04.012
- Stevens, J. R., & Hauser, M. D. (2004). Why be nice? Psychological constraints on the evolution of cooperation. *Trends in Cognitive Science*, *8*, 60–65.
- St. Pierre, A., Larose, K., & Dubois, F. (2009). Long-term social bonds promote cooperation in the iterated Prisoner's Dilemma. *Proceedings of the Royal Society: Biological Sciences*, *276*, 4223–4228.
- Taborsky, B., & Oliveira, R.F. (2012). Social competence: an evolutionary approach. *Trends in Ecology and Evolution*, *27*, 679–688.
- Thom, J. M., & Clayton, N. S. (2014). No evidence of temporal preferences in caching by Western scrub-jays (*Aphelocoma californica*). *Behavioural Processes*, *103*, 173–179. doi:10.1016/j.beproc.2013.12.010
- Tomback, D. F. (1998). Clark's Nutcracker (*Nucifraga columbiana*). In: A Poole (ed) *The birds of North America online*. Cornell Lab of Ornithology, Ithaca. Retrieved

from the Birds of North America online.

<http://bna.birds.cornell.edu/bna/species/331>. doi:10.2173/ bna.331

- Trivers, R. L. (1971). Evolution of reciprocal altruism. *The Quarterly Review of Biology*, *46*, 35–57.
- Vander Wall, S. B., & Jenkins, S. H. (2003). Reciprocal pilferage and the evolution of food-hoarding behavior. *Behavioral Ecology*, *14*, 656–667.
- Viana, D. S., Gordo, I., Sucena, É., & Moita, M. A. P. (2010). Cognitive and motivational requirements for the emergence of cooperation in a rat social game. *PLoS ONE*, *5*, e8483.
- Vonk, J., Brosnan, S. F., Silk, J. B., Henrich, J., Richardson, A. S., Lambeth, S. P., Schapiro, S. J., & Povinelli, D. J. (2008). Chimpanzees do not take advantage of very low cost opportunities to deliver food to unrelated group members. *Animal Behaviour*, *75*, 1757–1770.
- 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.
- Watts, D. P. (2002). Reciprocity and interchange in the social relationships of wild male chimpanzees. *Behaviour*, *139*, 343–370.
- Watts, D. P. & Mitani, J. C. (2002). Hunting and meat sharing by chimpanzees at Ngogo, Kibale National Park, Uganda. In C. Boesch, G. Hohmann & L. F. Marchant (Eds.), *Behavioural diversity in chimpanzees and bonobos* (pp. 244–255). New York, NY: Cambridge University Press.

Woolfenden, G. E. & Fitzpatrick, J. W. (1996). Florida scrub-jay (*Aphelocoma coerulescens*). In A. Poole (Ed.) The Birds of North America Online. Cornell Lab of Ornithology, Ithaca. Retrieved from the Birds of North America online: <http://bna.birds.cornell.edu/bna/species/228>. doi: 10.2173/bna.228

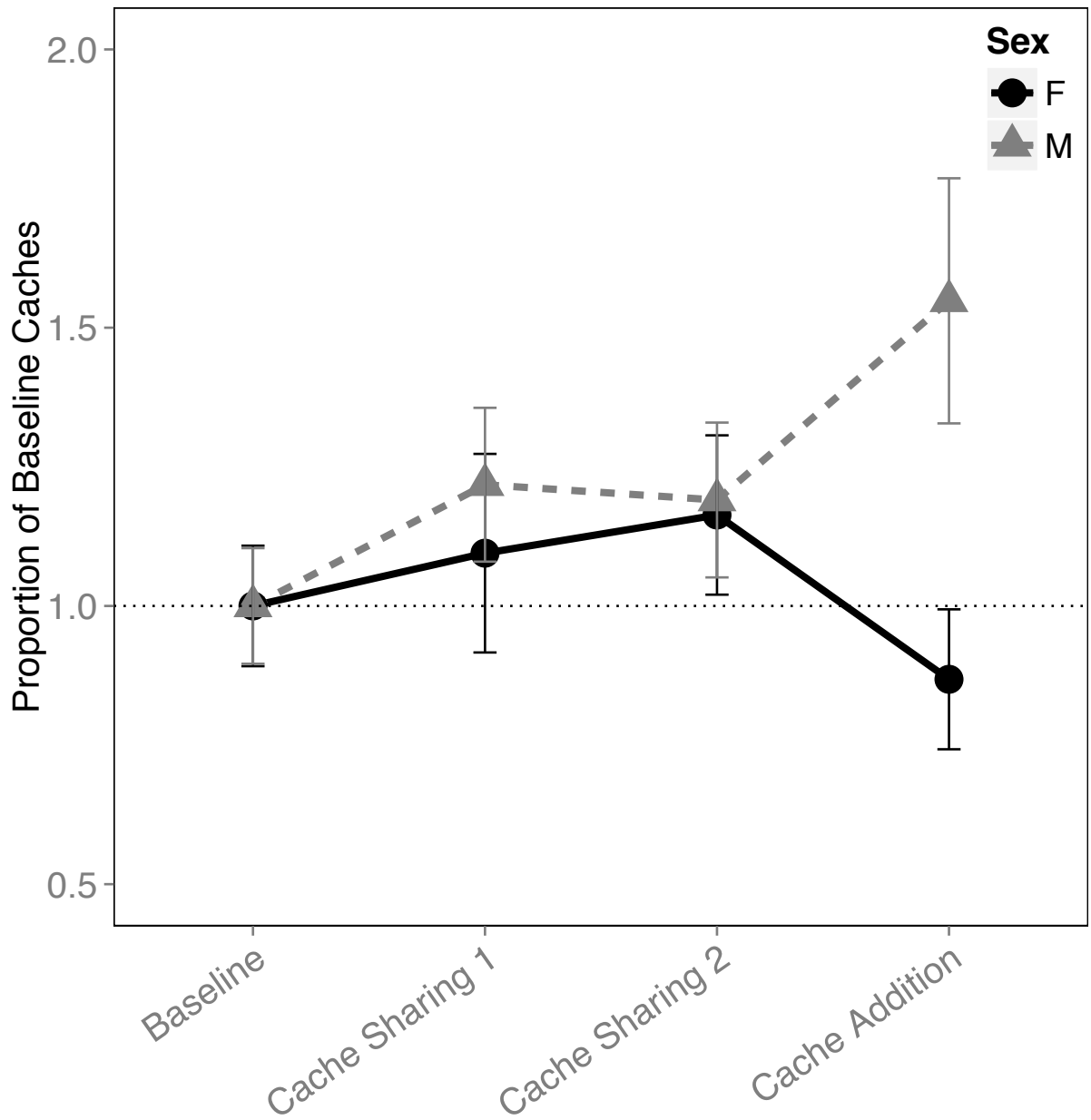


Figure 1. Proportion of baseline caches made (\pm SEM) during each block of six trials.

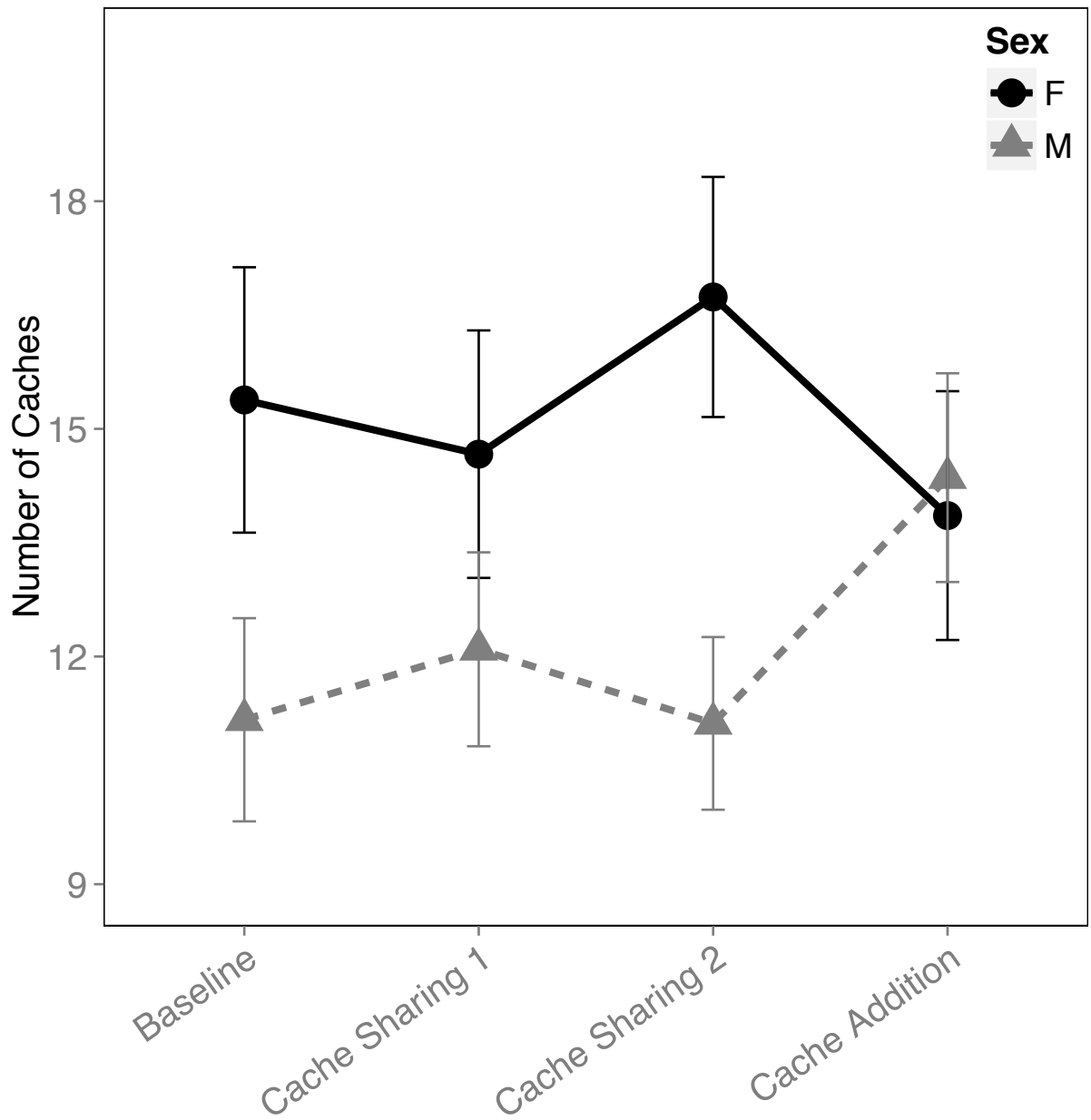


Figure 2. Mean number of caches made (\pm SEM) during each block of six trials.

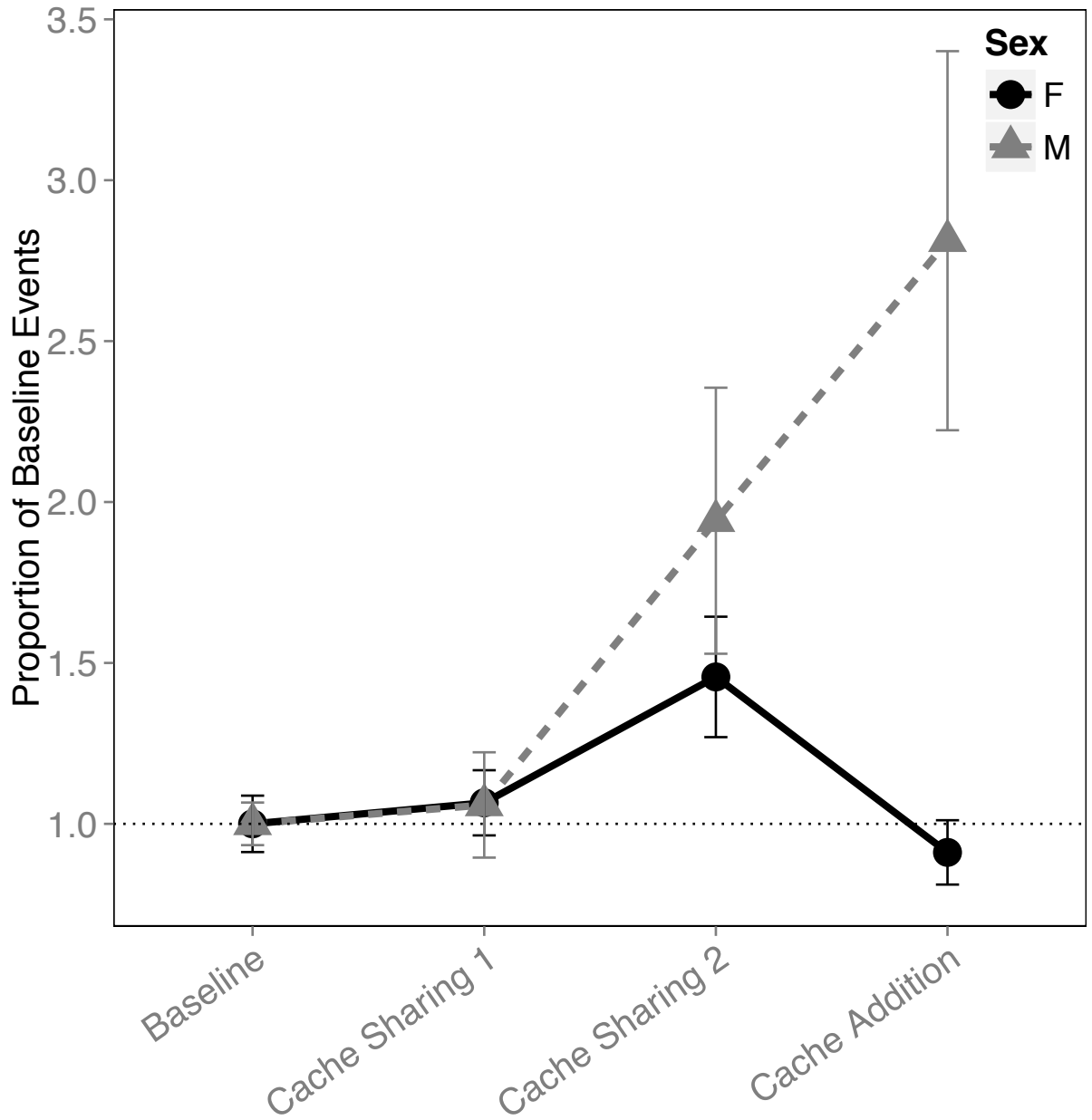


Figure 3. Proportion of baseline caching events (\pm SEM) during each block of six trials.

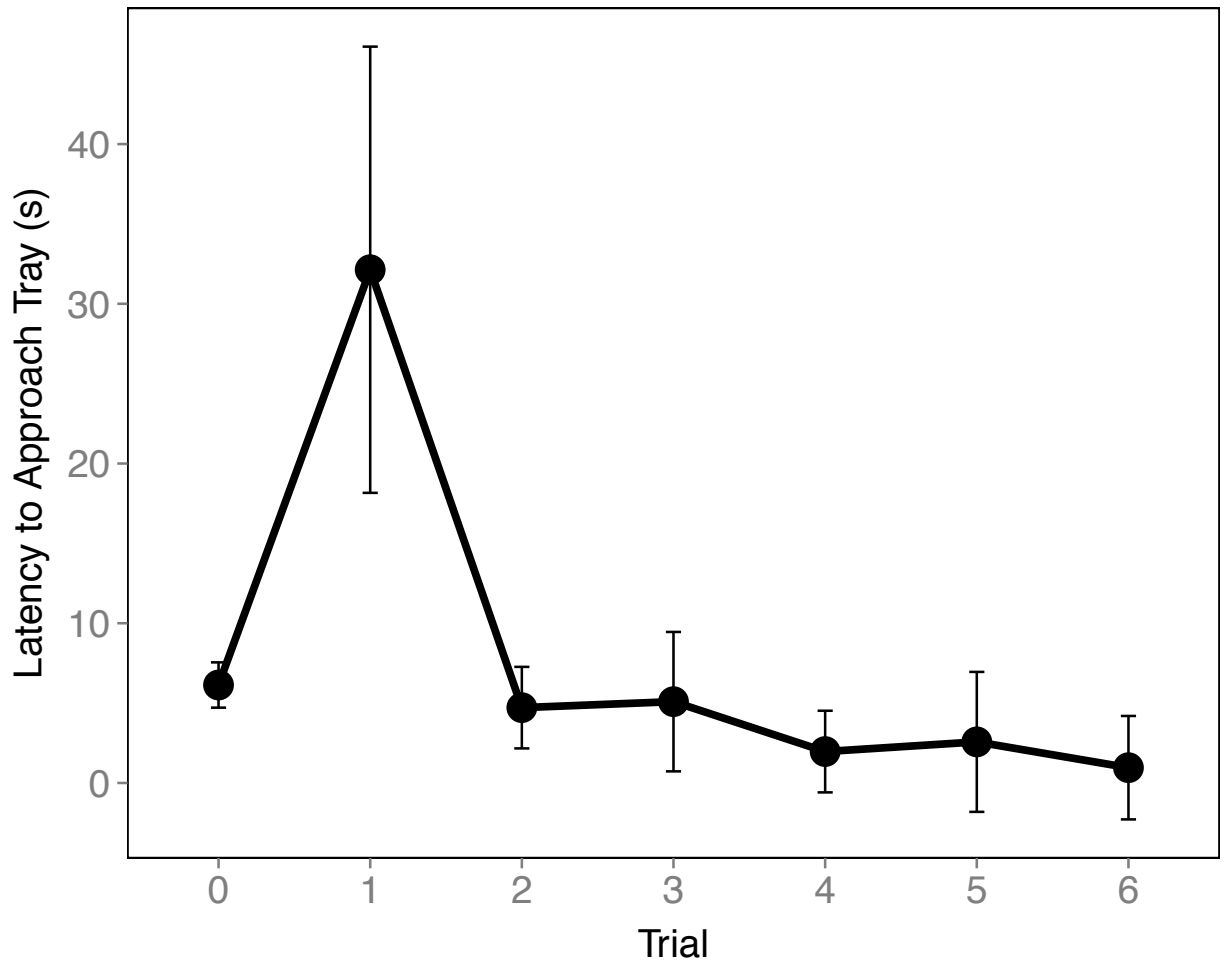


Figure 4. Mean latency to approach tray (\pm SEM) during the final Baseline trial (0) and the first six Cache Sharing trials.

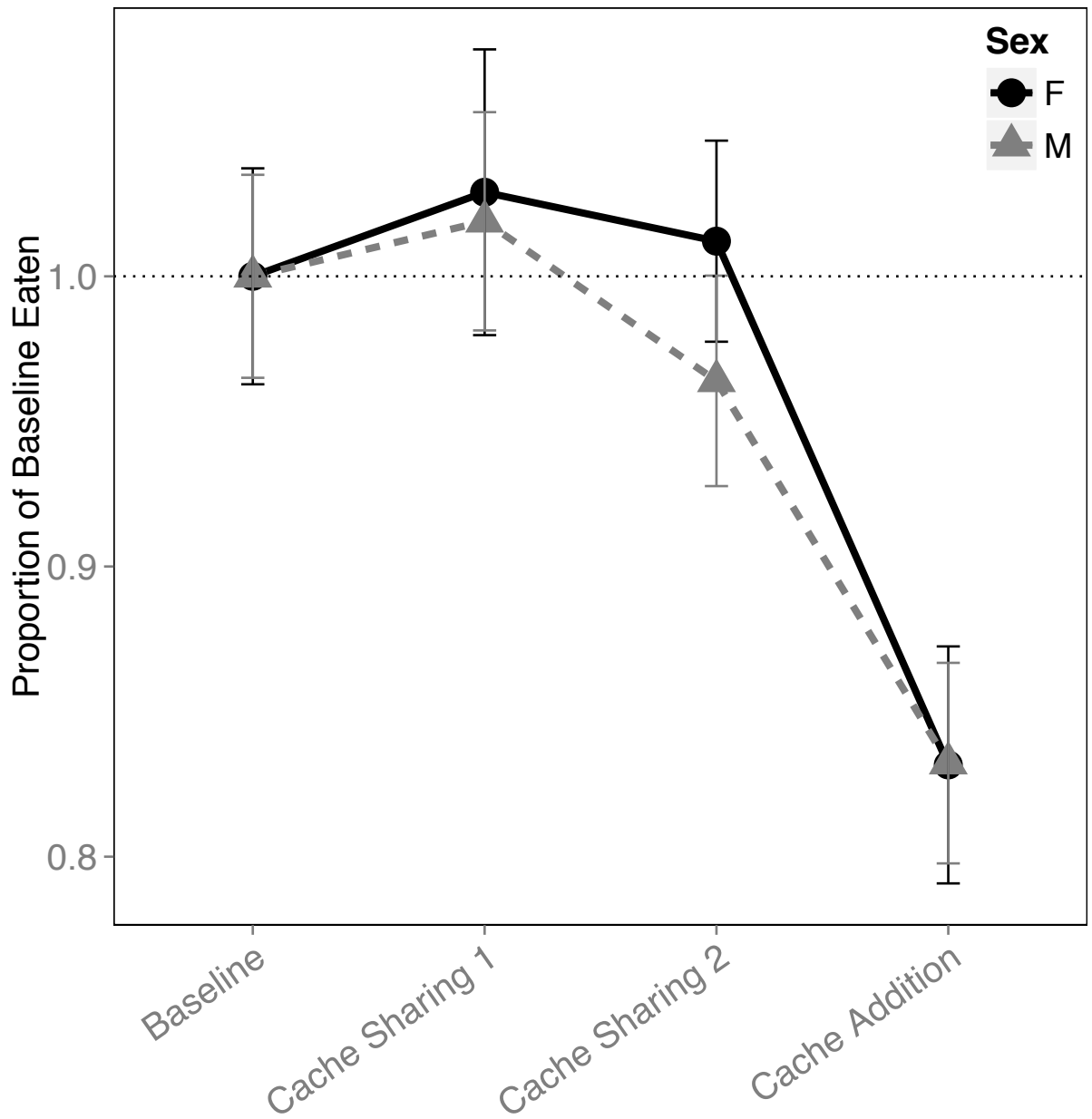


Figure 5. Proportion of baseline pine nuts eaten (\pm SEM) during each block of six trials.

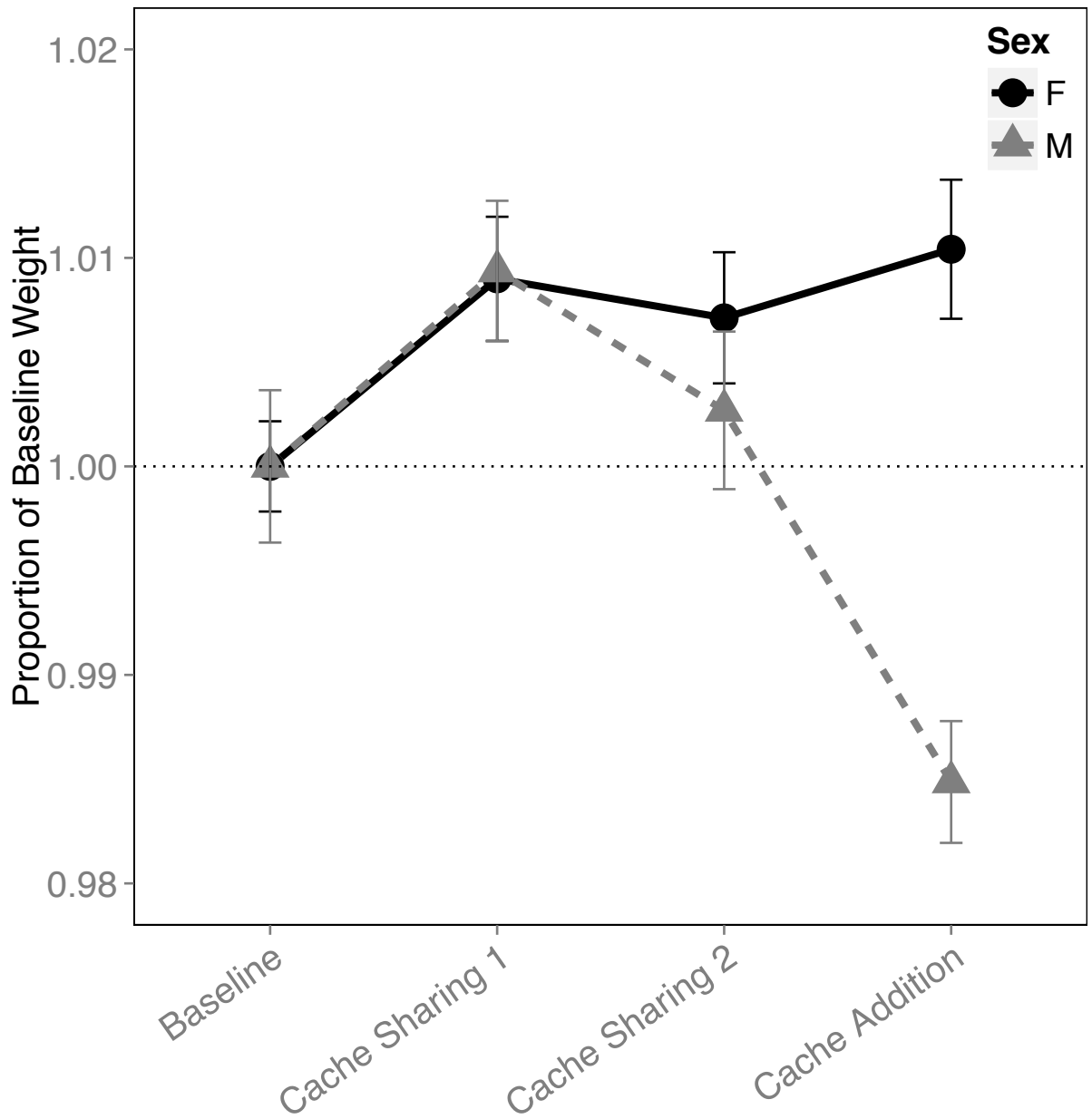


Figure 6. Proportion of baseline weight (\pm SEM) during each block of six trials.

Chapter 5: General Discussion

The evidence presented in Chapters 2 and 4, combined with previous research investigating the cognitive abilities of non-social corvids, suggests there is no generalized cognitive advantage for social corvids, even when measuring social cognition, which some variants of the social living hypotheses predict to be especially developed in social species (Byrne & Whiten, 1997). When confronted with the most cognitively demanding tasks, the nutcrackers, and non-social corvids in general, show considerable flexibility in adjusting to social problems.

In regards to mirror self-recognition, the results of Chapter 2 are as convincing, or more convincing, than evidence from social species that corvids can use mirrors for self-recognition. Both New Caledonian crows and jungle crows (relatively social species) have been tested for mirror use, with both species showing no indication of self-recognition, instead engaging in social behaviours upon exposure to a mirror (Kusayama et al., 2000; Medina et al., 2011). For species tested with the mark test, jackdaws showed no evidence of self-recognition (Soler et al., 2014), whereas a study of European magpies found two of five individuals showed self-recognition behaviours (Prior et al., 2008). As in Prior et al. (2008), two of the nutcrackers showed evidence of self-recognition with the regular mirror, however, six of the ten birds (including the aforementioned two) showed evidence of mirror use when the blurry mirror condition is considered. When combined with the caching task, all of the individuals showed an advantage for self-recognition with the blurry mirror. Not only did a high proportion of individuals show behaviours indicative of self-recognition compared to studies of other corvids (Prior et al., 2008) and great apes (Povinelli et al., 1993), but the current findings were also strengthened by the

convergence of results between the caching task and the mark test. Moreover, the results were not due to the birds simply using tactile cues, as suggested by Soler et al. (2014), as the nutcrackers ruffling behaviour was influenced more by visual cues than sensing the weight of the mark (Chapter 2, Extended Data Figure 6). Therefore, arguably the strongest evidence of self-recognition in corvids has been obtained by studying a non-social species; contrary to arguments that self-recognition should be most developed in social species (Bekoff & Sherman, 2003). Alternatively, some researchers have argued that some form of self-awareness is likely present in all animals (Spada, Aureli, Verbeek, & de Waal, 1995) and a recent theory has posited that self-awareness has origins in the need to simulate multiple alternative feeding opportunities (Hills & Butterfill, 2015), further suggesting that this ability need not be limited to social species. During foraging, animals are often required to choose between alternative future resource options, which vary according to quality and quantity. Hills and Butterfill (2015) proposed a model in which animals generate a rudimentary ‘self’ as a reference for differentiating motor routines simulated during prospective foraging at each resource cluster (queried from memory of learned clusters) from those actually carried out by the animal. Indeed, if a primitive self-awareness evolved to distinguish actual versus simulated actions, then this ability may be more broadly present among animals than suggested by results from the mark test, and certainly not limited by sociality.

In terms of cooperation, the results of Chapter 4 indicate that Clark’s nutcrackers are not bound by a species-typical tendency to suppress caching when confronted with atypical social contingencies that render cache suppression unnecessary. Additionally, the nutcrackers’ relatively non-social lifestyle did not preclude them from behaving

cooperatively. It should be noted that although this conclusion is based on the combination of all birds maintaining caching (unlike Chapter 2 and Clary & Kelly, 2010) and the increase in caching by the males during Cache Addition, the results should be interpreted with some caution, as there was no explicit ‘competitive condition’ contained within the experiment itself, during which the birds only experience cache loss with no offsetting caches received from the partner. Such a condition would have allowed for a direct comparison between competitive and cooperative situations and provided more definitive evidence as to whether the birds intentionally cooperated.

The conclusion that sociality may not be important for cooperation is also supported by comparisons between chimpanzees and bonobos, which unlike chimpanzees, are characterized by much greater intraspecies tolerance (Hare, Wobber, & Wrangham, 2012). When the cooperation of these two closely related species was compared, bonobos were found to be more willing to collaborate to obtain a clumped food reward, whereas cooperation in chimpanzees breaks down over time after the dominant individual starts to monopolize the joint resource (Hare, Melis, Woods, Hastings, & Wrangham, 2007). Therefore, although both species were initially able to cooperate, how that cooperation was maintained over time differed between the two species. Similarly, unlike human children (Tomasello, Carpenter, Call, Behne, & Moll, 2005), another highly social species, chimpanzees prefer to work alone, but if cooperation increases the payoff that can be achieved, this preference is reversed (Bullinger, Melis, & Tomasello, 2011). Likewise, the nutcrackers (at least the males) showed the most evidence of cooperation when the payoff from the partner was enhanced. Considering the evidence from both primates and my current results from

social caching with nutcrackers (Chapter 4), sociality is not a strict requisite for cooperation. Rather, both social and less-social species can possess the cognitive capacity for cooperation but different intraspecies interaction styles may regulate the circumstances under which cooperation occurs.

A Generalized Cognitive Advantage?

According to the social living hypotheses (Dunbar, 1998; Humphrey, 1976; Whiten & Byrne, 1997), living in large groups promoted the evolution of generalized intelligence, and for corvids specifically, it has been suggested that social species possess more flexible and generalizable cognitive abilities (Bond et al., 2007). Yet, for corvids, the evidence for a generalized cognitive advantage for social corvids is quite limited. Social corvids have been argued to outperform less social corvids in a variety of tasks including: serial reversal (Bond et al., 2007), observational learning (Templeton et al., 1999), observational spatial memory (Bednekoff & Balda, 1996a, b), and transitive inference (Bond et al., 2003). However, the results of these examples provide only equivocal support for the social living hypotheses and do not necessarily reinforce the position that social species have a generalized cognitive advantage over less social species. For instance, the findings that social pinyon jays, but not non-social nutcrackers, learn more quickly if first allowed to observe another bird solve a task (Templeton et al., 1999) would, ostensibly, support the social living hypotheses. Yet, overall the nutcrackers needed fewer trials to meet the learning criterion when solving a task individually, and no difference was found in number of trials needed for social learning between the species. Thus, this study indicates only that pinyon jays have a within-

species advantage for learning by observation, not a between-species generalized cognitive advantage over nutcrackers (as also argued by Templeton et al., 1999).

Bednekoff & Balda (1996a, b) argued that social species are superior at observational spatial memory due to findings that social pinyon jays and Mexican jays find the specific cache locations of others at better than chance levels after a 2-day delay, whereas nutcrackers only did so after a 1-day delay. That is, after a 2-day delay, when searching in a cluster of six holes containing a single cache, the Mexican jays made fewer errors than expected by chance. However, this interpretation is complicated by the finding that the Mexican jays did not enter clusters that contained a cache before entering empty clusters. Whereas nutcrackers, despite searching randomly when within a cluster containing a cache, still differentiated the clusters that contained caches from those that did not after two days. Therefore, all species studied seem to retain memory for the caches of others after two days, though whether specific locations or the general area is remembered may differ between species. These findings are further complicated by the fact that nutcrackers tended to make more caches, likely increasing interference and memory load effects, at least compared to Mexican jays (Bednekoff & Balda, 1996a).

Finally, Bond et al. (2003) found that highly social pinyon jays learned transitive inferences more rapidly and accurately than moderately social Western scrub jays. However, a more comprehensive comparative study found that non-social nutcrackers also performed transitive inferences better than the moderately social scrub jays, and as well as highly social pinyon jays and azure-winged magpies (Bond et al., 2010). Therefore, although social species may outperform less social species on any given task

(e.g., Bond et al., 2003, 2007), it is unlikely this indicates a generalized cognitive advantage, as predicted by the social living hypotheses.

Contrarily, nutcrackers outperform social species on other tasks, particularly those involving spatial memory (Balda & Kamil, 1989; Kamil, Balda, & Olson, 1994; Olson, Kamil, Balda, & Nims, 1995; see also Bond et al., 2010 for transitive inference), and show a variety of other cognitive traits that do not seem to be strongly influenced by sociality such as inhibition (Vernouillet, Anderson, Clary, & Kelly, 2016), inferential reasoning (Tornick & Gibson, 2013), and cerebral lateralization (Clary, Cheys, & Kelly, 2014). Furthermore, like social corvids, nutcrackers have been shown to be capable of other complex cognitive abilities such as episodic-like memory (Gould, Ort, & Kamil, 2012), numerical judgments (Rugani, Kelly, Szelest, Regolin, & Vallortigara, 2010; Tornick, Callahan, & Gibson, 2015) and gesture comprehension (Clary & Kelly, 2013; Tornick et al., 2011). Impressively, nutcrackers even learn abstract relational concepts (same/different) with fewer training exemplars than any tested non-human primate (Magnotti, Katz, Wright, & Kelly, 2015) and equivalent to the learning performance of highly social black-billed magpies (Magnotti, Wright, Leonard, Katz, & Kelly, 2016), further suggesting complex cognition is not exclusively dependent on living in large groups.

Alternatives to the Social Living Hypotheses

Accumulating research is indicating that other ecological factors, other than strictly the size of social groups, plays a large role in promoting cognitive abilities (Lefebvre, 2012). Even within primates, which show the strongest relationship between group size and brain size, the relationship may only exist in some lineages (haplorrhines

but not strepsirrhines: Navarrete & Laland, 2015), and a large phylogenetic analysis of inhibitory control (an executive function involved in many cognitive abilities) implicated dietary breadth over social group size as the best predictor of inhibition (MacLean et al., 2014). Similarly, within other mammals there seems to be considerable variation in the relationship between brain and body size, implicating different mechanisms according to each mammalian order (Jerison, 1955, 1961, 1973; Smaers et al., 2012). Instead, a multitude of factors such as home range size (Lefebvre, 2012), diet type and quality (Barton, 1999; Overington, Dubois, & Lefebvre, 2008), reliance on vision (Barton, 1998), need to innovate (Lefebvre, Reader, & Sol, 2004), mating system (Lemaître, Ramm, Barton, & Stockley, 2009; Pitnick, Jones, & Wilkinson, 2006), and habitat type (Jolicoeur, Pirlot, Baron, & Stephan, 1984; Schuck-Paim, Alonso, & Ottoni, 2008) likely play an interacting role (Lefebvre & Sol, 2008). For birds specifically, it has been found that species living in more seasonal and fluctuating environments have larger brains than those in stable environments (Schuck-Paim et al., 2008), likely because these environments are more cognitively demanding (*cognitive buffer hypothesis*: Allman, McLaughlin, & Hakeem, 1993). Additionally, when social factors have been related to group size in birds, species that form small groups and long-term pair bonds were found to have the largest brains (Emery, Seed, von Bayern, & Clayton, 2007). Therefore, it seems the nature and quality of the relationships a species engages in is more important than simply the number of individuals likely to be encountered, and there is no linear benefit from living in groups of hundreds or thousands of individuals where the likelihood of repeat encounters is low (Emery et al., 2007). Indeed, repeat encounters

with familiar individuals are likely especially important for the development of social cognition (Adolphs, 2009; Singer et al., 2006).

Confronted with incompatible findings, the *social brain hypothesis* has since undergone modification to make it more consistent with recent findings (Dunbar, 2009). Although some success has been reported using alternative measures of social group size, such as grooming clique size (Kudo & Dunbar, 2001), clusters of regular associating individuals (Pérez-Barberia, Shultz, & Dunbar, 2007), or degree of fission-fusion (Amici, Aureli, & Call, 2008), perhaps the most promising modification has been a focus on the formation of pairbonds (Dunbar, 2009). Dunbar (2009) has argued that the cognitive demands of maintaining pairbonds, which require close social coordination between individuals, may be the crucial aspect responsible for the evolution of large ‘social’ brains (see also Emery et al., 2007). Dunbar argues this interpretation is more compatible with existing data showing pairbonds are related to brain size in both birds (Dunbar & Shultz, 2007; Emery et al., 2007) and mammals (Lemaître et al., 2009; Pitnick et al., 2006). Further, Dunbar accounts for the aberrant findings from primates, where a stronger brain size-body size relationship is found, by speculating that early in their evolution primates generalized the cognitive mechanisms required for maintaining successful pairbonds to other group members to facilitate social living.

Given the plethora of factors that have been implicated in promoting large brains and cognitive abilities, how do nutcrackers fit into these theoretical frameworks? Based on their ecology, it seems nutcrackers possess a number of life history traits that would predict large brains and cognitive complexity. In accordance with the *cognitive buffer hypothesis*, nutcrackers reside in high elevation environments throughout the Rocky

mountains that undergo severe seasonal changes (Tomback, 1998). To cope with cold, harsh winters with sparse resources, nutcrackers rely almost exclusively on their cached pine nuts for sustenance, but then feed opportunistically on a variety of food types during the spring and summer (Tomback, 1998). In accordance with Dunbar's (2009) pairbond hypothesis, nutcrackers form long-term monogamous pairs with extensive bi-parental care (Dixon, 1934), with both males and females possessing a brood patch for incubating young (Mewaldt, 1952). Young birds are characterized by long developmental periods, during which they learn specialized foraging techniques (Tomback, 1978, 1998; Vander Wall & Hutchins, 1983). In accordance with Emery et al.'s (2007) findings that relative brain size follows a parabolic function with avian group sizes, nutcrackers only form small groups (Hutchins & Lanner 1982; Mewaldt 1948; Tomback 1977; Vander Wall & Hutchins 1983) aligning them with group classifications associated with larger brains. Lastly, nutcrackers' dependence on cached food has been argued to have promoted their cognitive representation abilities (Bond et al., 2010) and may necessitate nutcrackers to be particularly sensitive to the social conditions while caching. Considering the high rates of pilferage that occur in the wild from both conspecifics and heterospecifics (Vander Wall & Jenkins, 2003), it is unlikely that a less social species would be sheltered from the risk of cache theft. Indeed, Steller's jays have been reported to wait for nutcrackers to cache in their territory and then pilfer the caches once the nutcrackers have left (Tomback, 1978). Therefore, although enhanced cognitive complexity is not predicted according to the social living hypotheses, nutcrackers are characterized by a number of other traits that are thought to benefit cognitive and neural development.

Adaptive Specializations vs. General Processes

Considering the combination of life history traits that predict complex cognition and the cognitive sophistication of nutcrackers and other non-social species, what does this tell us about the nature of intelligence? Often, this question is presented as between two competing possibilities: adaptive specialization and general processes (Macphail & Bolhuis, 2001). Proponents of adaptive specialization argue that ecology shapes the cognitive abilities of species in much the same way that ecology shapes the morphology and physiology of species to adapt them to their evolutionary environments (Kamil, 1994; Shettleworth, 2009). Following from that approach, neuroecology predicts that brain regions supporting behaviours demanded by a species' ecological niche become enlarged or gain specialized circuitry over evolutionary time. Advocates for general processes argue that cognition is characterized by fundamental learning and memory processes that are used to solve a variety of problems, are held broadly across species, and function similarly regardless of ecological demands, though perceptual processes may be selected upon according to ecological pressures (Bitterman, 2000; Macphail & Bolhuis, 2001).

Evidence for adaptive specializations largely comes from two sources: a relationship between hippocampus size and spatial memory use, and the size of song control nuclei and vocal repertoire. Though disputed by some (Brodin & Lundborg, 2003; Macphail & Bolhuis, 2001), the balance of evidence supports that species with more demands on spatial memory (caching or brood parasitic species) have larger hippocampal volumes or greater hippocampal plasticity than animals with less spatial memory demands (Healy, de Kort, & Clayton, 2005; Hoshooley & Sherry, 2007; Sherry &

Hoshooley, 2010). Similarly, birds with larger vocal repertoires typically have larger brain regions controlling the learning and production of calls and songs (Brenowitz, 1997; DeVoogd, Krebs, Healy, & Purvis, 1993; Garamszegi & Eens, 2004).

Those who favour general processes criticize the adaptive specialization approach of trying to use function to explain cause – two independent concepts that cannot logically be used to explain one another (Macphail & Bolhuis, 2001). In other words, the critique is that the adaptationist approach suggests differences in functional aspects of species (e.g., presence or absence of food-storing behaviour) indicate qualitatively different causes (e.g., different learning and memory processes) are responsible for each species' behaviour, when in fact the presence or absence of a function does nothing to inform its cause. In defense of the adaptationist approach, supporters argue that they simply use function as a guide for identifying plausible causes (Sherry, 2005). Furthermore, adaptive specializations are, at times, not found when they would be expected to occur. For instance, a comparison between tool-using and non-tool-using finches found no advantage for the tool-using birds (both within and between species) to solve an assortment of physical cognition tasks (Teschke, Cartmill, Stankewitz, & Tebbich, 2011). Proponents of general processes instead argue that trends between complex lifestyles and larger brains are better explanations for the evolution of brains which are capable of general intelligence (Lefebvre & Sol, 2008), a stance bolstered by findings that cognitive traits are correlated across a variety of domains (e.g., brain size, innovation, and tool use: Lefebvre, Nikolakakis, & Boire, 2002; Lefebvre, Reader, & Sol, 2004; Reader & Laland, 2002).

Applying these concepts to corvids illustrates that although the above hypotheses are usually presented as mutually exclusive, it is likely they both function concurrently to adapt cognition and brains. As discussed, both social and non-social corvids share an aptitude across a number of cognitive domains and their general intelligence can be further illustrated by returning to the example of tool use. Among corvids, only New Caledonian crows are known to habitually use tools in nature (Hunt, 1996), and laboratory studies show they understand the physical properties of the tools used (Chappell & Kacelnik, 2002, 2004; Taylor, Hunt, Medina, & Gray, 2009). However, when confronted with laboratory tasks that require tool use, other non-tool-using corvids are also capable of using tools to solve physical problems (Bird & Emery, 2009; Cheke, Bird, & Clayton, 2011; Seed, Tebbich, Emery, & Clayton, 2006; Tebbich, Seed, Emery, & Clayton, 2007). These results suggest tool-use is a product of pre-existing general cognitive abilities, which result in tool-use only if required by a species' ecology (Bird & Emery, 2009; Cheke et al., 2011). That said, there seems to also be specific adaptive specializations that may be attributed to social living (e.g., observational learning, Templeton et al., 1999) or cache reliance (Healy et al., 2005). Clark's nutcrackers may have benefited both from the general trend for increased cognitive abilities in corvids, likely driven by their need to adapt to new environments and feeding opportunities during their evolution, but also adaptive specializations in specific cases such as spatial memory, where strong selection pressures exist to improve memory for accurate recall of cache site locations. The findings of this dissertation do not rule out adaptive specializations, though they do indicate they are not featured prominently in the broad social cognitive abilities of corvids.

Conclusions

In summary, the social cognitive abilities of Clark's nutcrackers are presumably derived from a general intelligence exhibited by corvids afforded to them by large brains that have deviated from other avian groups (Jerison, 1973; Iwaniuk & Nelson, 2003; Emery et al., 2007; Rehkämper, Frahm, & Zilles, 1991). The reason for the increase in brain size is likely due to an interaction of many ecological variables that promote brain enlargement, and although social factors are involved, these alone do not seem to be strong indicators of variation in brain size or cognitive ability within corvids. The nutcrackers have many life history traits that likely fostered their impressive neural and cognitive traits – traits that grant them considerable behavioural flexibility to cope with a variety of challenges. From self-recognition (Chapter 2) to social cognition (Chapter 4), nutcrackers seem capable of differentiating their 'self' from others, and use this distinction to alter their behaviour in beneficial ways, even when the behaviour measured could be prone to species-typical tendencies. The impressive social cognition exhibited by nutcrackers runs counter to the predictions made by the social living hypotheses, and confirm that there is more than one evolutionary route to complex cognitive abilities.

Chapter 6: Future Directions

Although to this point I have argued that social living is not a panacea for explaining complex cognitive abilities in animals, social living is assuredly one piece of the evolutionary puzzle. So, the question remains as to what cognitive advantages social living provides and are there adaptive specializations to cognition that could result from living in social groups? The general intelligence of corvids seems to allow them to solve social problems regardless of sociality, though this does not preclude adaptive specializations for specific abilities. The results of Templeton et al. (1999) showing that pinyon jays, but not nutcrackers, have a within-species advantage to learn socially hints that adaptive specializations may result from living in social groups. However, it is still unclear whether observational learning is an adaptive specialization (Heyes, 2012) or whether the conditions under which social and non-social species learn from others differ.

Given the generalized intelligence demonstrated by relatively non-social species it would be surprising if they were heavily restricted in when they could use social information, especially when considering that some types of social information would benefit both social and non-social species equally. For example, crows have been found to use the location and predators present by dead conspecifics to facilitate learning of the circumstances of the bird's death (Swift & Marzluff, 2015). The use of such social information should be selected for regardless of sociality, as the cost of learning individually about predators is too high (Boyd & Richerson, 1985, 1988; Feldman, Aoki, & Kumm, 1996; Laland, 2004). Therefore, the question becomes: are non-social species unable to use observational learning or is the difference more relative, such that the

difference between social and non-social species lies in when and from whom social information is used?

Tendency to use Social Information Sources

Social and non-social species may differ in from whom they acquire information. Social learning can be facilitated if learning from a mate (White & Galef, 1999, 2000; Galef & White, 1998), a familiar group member (Swaney, Kandal, Capon, Brown, & Laland, 2001), or by following an individual known to be informed (Menzel, 1973, 1974). Considering that less social species have fewer group members that can provide social information, these species may be biased in using information from familiar or ‘trusted’ individuals, such as the pairbonded mate, whereas social species use social information more indiscriminately due to the availability of this information from unrelated or unfamiliar individuals.

Social and non-social species may also differ in their sensitivity to the relative costs and benefits associated with social learning. Indeed, the cost of social information relative to individual learning has been shown to regulate the choices of European Starlings (Templeton & Giraldeau, 1996), and callitrichid monkeys use social information only when a task is challenging (Day, 2003; Day, Coe, Kendal, & Laland, 2003; Laland, 2004). Evidence comparing socialized dogs and wolves also suggest that species may differ in their threshold for seeking out social information. For instance, Miklósi et al. (2003) found that when presented with an unsolvable problem, wolves tended to persevere on solving the task, whereas dogs would stop to look at a nearby human, likely to solicit help or seek social information. This species difference was interpreted as a consequence of the domestication of dogs, as their behaviour has been

shaped by selective breeding to facilitate communication with humans. As of yet, no studies have compared social and non-social species while titrating the costs and payoffs associated with social and individual learning. Studying observational learning across social and non-social species using tasks of varying difficulty and with varying reward values would be particularly informative for addressing this unresolved issue.

The Cognitive Advantages and Disadvantages of Groups

Although social learning is often presented as a more efficient means of learning, this need not be the case (Galef, 1995; Laland, 2004). Using social information can lead to the adoption of suboptimal behaviours if an inefficient solution invades a group (Laland & Williams, 1998; Pongrácz, Miklósi, Kubinyi, Topál, & Csányi, 2003). In fact, learning individually can offer a substantial advantage in these situations, as evidenced by guppies selecting more efficient travel routes when tested alone than when tested in a group with a preference for a longer route (Laland & Williams, 1998). Additionally, social animals may abandon solvable tasks too quickly, in favour of seeking a social solution that may not exist, and if too many individuals adopt this strategy, knowledge transmission breaks down (Laland, 2004). If less social species persist longer on a task or are better able to learn individually, this would explain the results of Miklósi et al. (2003), in which wolves perseverated on an unsolvable task, and Templeton et al. (1999), in which nutcrackers learned tasks individually faster than social pinyon jays. Therefore, it is conceivable that more social species make more regular use of social learning opportunities, however this does not necessitate a cognitive advantage, nor does it guarantee better decision-making.

Although efficient behaviour or problem solving is not a guaranteed outcome of living in social groups, under the right conditions it confers a significant advantage. Individuals living in a social group have more opportunities to take advantage of cultural transmission of knowledge and by exploiting the collective “wisdom of the crowds” can often make decisions more accurately than making them individually (Krause, Ruxton, & Krause, 2010; Seeley, 2010; Levenson, Krupinski, Navarro, & Wasserman, 2015; Surowiecki, 2005). However, it is unclear whether this advantage results in a direct cognitive benefit to the individual or whether individuals of social living species simply appear more ‘intelligent’ because of behaviours produced by the group. For instance, by using quorum decision-making, ant colonies have been found to outperform individuals when choosing the better of two nest sites (Sasaki, Granovskiy, Mann, Sumpter, & Pratt, 2013). A similar advantage for group decision-making has been reported for fish when discriminating stimuli (Ward, Sumpter, Couzin, Hart, & Krause, 2008) and for homing pigeons attempting to select the most efficient route (Biro, Sumpter, Meade, & Guilford, 2006). This raises the possibility that social species may appear to be capable of more cognitively complex abilities because of group-derived behaviours, though when tested individually show no advantage over less social species. Indeed, even Humphrey (1976) acknowledged being part of a group could allow individuals to exploit pre-existing techniques, rather than having to produce imaginative solutions themselves. Thus, this highlights the need for further study of what information is used by social and non-social animals, and under which circumstances ‘intelligent’ behaviour emerges, whether through individual ingenuity or by adopting group-derived behaviours.

The Role of ‘Pairbond’ Cognition

Although Dunbar’s (2009) hypothesis that monogamous pairbonds promote large brains is promising, in that this interpretation fits more of the data from more species, it has yet to be rigorously tested (by both brain *and* cognitive measures) and should be applied cautiously as a universal explanation for the evolution of cognition. As discussed in Chapter 5, cognitive abilities can be promoted by a variety of ecological influences and the claim that primates are unique in how they cognize dyadic relationships needs to be reconciled with animal groups with similar social behaviours (yet lack the strong relationship between group size and brain size), such as corvids. Research into the social life of ravens in particular has revealed these birds, like primates, form social bonds with non-mates (Bugnyar, 2013). Similar to chimpanzees, relationship quality of ravens is defined by three components (value, compatibility, and security: Fraser & Bugnyar, 2010a). Furthermore, the valence of raven relationships predicts their behaviour in conflict situations with reciprocal agonistic support shown between those that have allopreened (Fraser & Bugnyar, 2012), post-conflict reconciliation between opponents with valuable relationships (Fraser & Bugnyar, 2011), and consolation provided by both affiliated bystanders, as well as third parties if the conflict was severe (Fraser & Bugnyar, 2010b). Hence, corvid social cognitive abilities may not be based entirely on the demands imposed by their caching interactions and not limited to those contexts either. Again however, this is true of both social and non-social corvids. For instance, male Eurasian jays have recently been reported to infer the ‘desire state’ of their pairbonded mate (Ostojić, Shaw, Cheke, & Clayton, 2013; Ostojić et al., 2014). This was shown by allowing the male to provision the female after the female was satiated on one of two

food types. Males provided the female with the food type with which the female was not sated, despite not being allowed to view which food the female had eaten, and independent of the males own eating preference or motivational state. Additional comparative work of this nature would be particularly informative for elucidating the importance of pairbonds in facilitating complex social cognitive abilities. Specifically, comparisons of the social cognition of paired and unpaired individuals (or birds that have been paired for varying durations) could be used to evaluate whether the pairbonding experience promotes perspective taking in both breeding and non-breeding contexts.

The Fate of the Social Living Hypotheses

The above example demonstrating the convergence between primate and raven social systems highlights the importance of studying the cognition of a wide-variety of species, so that theories regarding the evolution of intelligence do not become primate-centric. Though it is often easier to recognize ‘intelligence’ in the behaviours of species that most resemble humans, this bias should not be represented in theories developed to explain complex cognitive abilities that are clearly more widespread than the primate lineage. Adopting a more comparative approach on both the theoretical and experimental level will be the most productive avenue for explicating the evolutionary paths that animals, including humans, took to acquiring their specific cognitive abilities.

References

- Adolphs, R. (2009). The social brain: neural basis of social knowledge. *Annual Review of Psychology, 60*, 693–716. doi:10.1146/annurev.psych.60.110707.163514
- Allman, J. M., McLaughlin, T., & Hakeem, A. (1993). Brain weight and life span in primate species. *Proceedings of the National Academy of Sciences of the United States of America, 90*(1), 118-122.
- Amici, F., Aureli, F., & Call, J. (2008). Fission-fusion dynamics, behavioral flexibility, and inhibitory control in primates. *Current Biology, 18*(18), 1415–1419. doi:10.1016/j.cub.2008.08.020
- Balda, R. P., & Kamil, A.C. (1989). A comparative study of cache recovery by three corvid species. *Animal Behaviour, 38*, 486–495. doi:10.1016/S0003-3472(89)80041-7
- Barton, R. A. (1998). Visual specialization and brain evolution in primates. *Proceedings of the Royal Society of London Series B: Biological Sciences, 265*(1409), 1933-1937.
- Barton, R. A. (1999). The evolutionary ecology of the primate brain. In P. C. Lee (Ed.), *Comparative primate socioecology* (pp. 167-194). Cambridge, UK: Cambridge University Press.
- 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.
- Bekoff, M., & Sherman, P. W. (2003). Reflections on animal selves. *Trends in Ecology and Evolution*, *19*, 176–180.
- Bird, C. D., & Emery, N. J. (2009). Insightful problem solving and creative tool modification by captive nontool-using rooks. *Proceedings of the National Academy of Sciences, U.S.A.*, *106*, 10370e10375.
- Biro, D., Sumpter, D. J. T., Meade, J., & Guilford, T. (2006). From compromise to leadership in pigeon homing. *Current Biology*, *16*(21), 2123–2128.
- Bitterman, M. E. (2000). Cognitive evolution: a psychological perspective. In C. M. Heyes & L. Huber (Eds.), *The evolution of cognition* (pp. 61–79). Cambridge, MA: MIT Press.
- Bond, A. B., Kamil, A. C., & Balda, R. P. (2003). Social complexity and transitive inference in corvids. *Animal Behaviour*, *65*(3), 479–487.
doi:10.1006/anbe.2003.2101
- Bond, A. B., Kamil, A. C., & Balda, R. P. (2007). Serial reversal learning and the evolution of behavioral flexibility in three species of North American corvids (*Gymnorhinus cyanocephalus*, *Nucifraga columbiana*, *Aphelocoma californica*). *Journal of Comparative Psychology*, *121*(4), 372–9. doi:10.1037/0735-7036.121.4.372

- Bond, A. B., Wei, C. A., & Kamil, A. C. (2010). Cognitive representation in transitive inference: A comparison of four corvid species. *Behavioural Processes*, 85(3), 283–292. doi:10.1016/j.beproc.2010.08.003
- Boyd, R., & Richerson, P. J. (1985). *Culture and the evolutionary process*. Chicago, IL: University of Chicago Press.
- Boyd, R., & Richerson, P. J. (1988). An evolutionary model of social learning: The effects of spatial and temporal variation. In T. Zentall & B. G. Galef (Eds.), *Social learning: A psychological and biological approach* (pp. 29-48). Hillsdale, NJ: Erlbaum.
- Brenowitz, E. A. (1997). Comparative approaches to the avian song system. *Journal of Neurobiology*, 33, 517–531.
- Brodin, A., & Lundborg, K. (2003). Is hippocampal volume affected by specialization for food hoarding in birds? *Proceedings of the Royal Society of London B: Biological Sciences*, 270, 1555–1563
- Bugnyar, T. (2013). Social cognition in ravens. *Comparative Cognition & Behavior Reviews*, 8, 1–12. doi:10.3819/ccbr.2013.80001
- Bullinger, A. F., Melis, A. P., Tomasello, M. (2011). Chimpanzees, *Pan troglodytes*, prefer individual over collaborative strategies towards goals. *Animal Behaviour*, 82, 1135–1141. doi:10.1016/j.anbehav.2011.08.008

Byrne, R. W., & Whiten, A. (1997). Machiavellian intelligence. In A. Whiten & R. W.

Byrne (Eds.), *Machiavellian intelligence II*. Cambridge, UK: Cambridge

University Press.

Chappell, J., & Kacelnik, A. (2002). Tool selectivity in a non-primate, the New

Caledonian crow (*Corvus moneduloides*). *Animal Cognition*, 5(2), 71–78.

doi:10.1007/s10071-002-0130-2

Chappell, J., & Kacelnik, A. (2004). Selection of tool diameter by New Caledonian Crows

Corvus moneduloides. *Animal Cognition*, 7, 121–127.

Cheke, L. G., Bird, C. D., & Clayton, N. S. (2011). Tool-use and instrumental learning in the Eurasian jay (*Garrulus glandarius*). *Animal Cognition*, 14, 441–455.

doi:10.1007/s10071-011-0379-4

Clary, D., & Kelly, D. M. (2013). Are Clark's nutcrackers (*Nucifraga columbiana*) able to discriminate knowledge states of human experimenters during an object-choice task? *Evolutionary Psychology*, 11(3), 628–646.

Clary, D., Cheys, A., & Kelly, D. M. (2014). Pattern of visuospatial lateralization in two corvid species, black-billed magpies and Clark's nutcrackers. *Behavioural*

Processes, 107, 94–98. doi:10.1016/j.beproc.2014.07.020

Day, R. L. (2003). *Innovation and social learning in monkeys and fish: Empirical findings and their application to reintroduction techniques* (Unpublished doctoral dissertation). University of Cambridge, UK.

- 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.
- DeVoogd, T. J., Krebs, J. R., Healy, S. D., & Purvis, A. (1993). Relations between song repertoire size and the volume of brain nuclei related to song-comparative evolutionary analyses amongst oscine birds. *Proceedings of the Royal Society of London B: Biological Sciences*, *254*, 75–82.
- Dixon, J. B. (1934). Nesting of the Clark Nutcracker in California. *Condor*, *36*, 229-234.
- Dunbar, R. I. M. (1998). The social brain hypothesis. *Evolutionary Anthropology*, *6*, 178-190.
- Dunbar, R. I. M. (2009). The social brain hypothesis and its implications for social evolution. *Annals of Human Biology*, *36*(5), 562–572.
doi:10.1080/03014460902960289
- Dunbar, R. I. M., & Shultz, S. (2007). Evolution in the social brain. *Science*, *317*(5843), 1344–1347. doi:10.1126/science.1145463
- 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*(1480), 489-505.

- Feldman, M. W., Aoki, K., & Kumm, J. (1996). Individual versus social learning: Evolutionary analysis in a fluctuating environment. *Anthropological Science, 104*, 209-232.
- Fraser, O. N., & Bugnyar, T. (2010a). Do ravens show consolation? Responses to distressed others. *PLoS ONE, 5*(5), e10605. doi:10.1371/journal.pone.0010605
- Fraser, O. N., & Bugnyar, T. (2010b). The quality of social relationships in ravens. *Animal Behaviour, 79*(4), 927–933. doi:10.1016/j.anbehav.2010.01.008
- Fraser, O. N. & Bugnyar, T. (2011). Ravens reconcile after conflicts with valuable partners. *PLoS ONE, 6*, e18118.
- Fraser, O. N., & Bugnyar, T. (2012). Reciprocity of agonistic support in ravens. *Animal Behaviour, 83*, 171–177. doi:10.1016/j.anbehav.2011.10.023
- Galef, B. G., Jr. (1995). Why behaviour patterns that animals learn socially are locally adaptive. *Animal Behaviour, 49*, 1325-1334.
- Galef, B. G., Jr., & White, D. J. (1998). Mate-choice copying in Japanese quail, *Coturnix coturnix japonica*. *Animal Behaviour, 55*, 545-552.
- Garamszegi, L. Z., & Eens, M. (2004). Brain space for a learned task: strong intraspecific evidence for neural correlates of singing behavior in songbirds. *Brain Research Reviews, 44*, 187–193.

- Gould, K. L., Ort, A. J., & Kamil, A. C. (2012). Do Clark's nutcrackers demonstrate what-where-when memory on a cache-recovery task? *Animal Cognition*, *15*(1), 37–44. doi:10.1007/s10071-011-0429-y
- Hare, B., Melis, A. P., Woods, V., Hastings, S., & Wrangham, R. (2007). Tolerance allows bonobos to outperform chimpanzees on a cooperative task. *Current Biology*, *17*, 619–623. doi:10.1016/j.cub.2007.02.040
- Hare, B. A., Wobber, V., & Wrangham, R. (2012). The self-domestication hypothesis: evolution of bonobo psychology is due to selection against aggression. *Animal Behaviour*, *83*(3), 573–585. doi:10.1016/j.anbehav.2011.12.007
- Healy, S. D., de Kort, S. R., & Clayton, N. S. (2005). The hippocampus, spatial memory and food hoarding: a puzzle revisited. *Trends in Ecology & Evolution*, *20*(1), 17–22. doi:10.1016/j.tree.2004.10.006
- Heyes, C. (2012). What's social about social learning? *Journal of Comparative Psychology*, *126*(2), 193–202. doi:10.1037/a0025180
- Hills, T. T., & Butterfill, S. (2015). From foraging to auto-noetic consciousness: The primal self as a consequence of embodied prospective foraging. *Current Zoology*, *61*(2), 368–381.
- Hoshooley, J. S., & Sherry, D. F. (2007). Greater hippocampal neuronal recruitment in food-storing than in non-food-storing birds. *Developmental Neurobiology*, *67*, 406–414.

Humphrey, N. K. (1976). The social function of intellect. In P. P. G. Bateson & R. A. Hinde (Eds.) *Growing points in ethology* (pp. 303–317). Cambridge, UK:

Cambridge University Press.

Hunt, G. R. (1996). Manufacture and use of hook-tools by New Caledonian crows.

Nature, 379(18), 249–251. doi:10.1038/379249a0

Hutchins, H. E. & Lanner, R. M. (1982). The central role of Clark's Nutcracker in the dispersal and establishment of whitebark pine. *Oecologia*, 55, 192-201.

Iwaniuk, A. N., & Nelson, J. E. (2003). Developmental differences are correlated with relative brain size in birds: a comparative analysis. *Canadian Journal of Zoology*, 81(12), 1913–1928.

Jerison, H. J. (1955). Brain to body ratios and the evolution of intelligence. *Science*, 121(3144), 447-449.

Jerison, H. J. (1961). Quantitative analysis of evolution of brain in mammals. *Science*, 133(345), 1012.

Jerison, H. J. (1973). *Evolution of the brain and intelligence*. New York, NY: Academic Press.

Jolicoeur, P., Pirlot, P., Baron, G., & Stephan, H. (1984). Brain structure and correlation patterns in insectivora, chiroptera, and primates. *Systematic Zoology*, 33(1), 14-29.

- Kamil, A. C. (1994). A synthetic approach to the study of animal intelligence. In L. A. Real (Ed.), *Behavioral mechanisms in evolutionary ecology* (pp. 11–45). Chicago, IL: Chicago University Press.
- Kamil, A.C., Balda, R.P., & Olson, D.J. (1994). Performance of four seed-caching corvid species in the radial maze analog. *Journal of Comparative Psychology*, *108*, 385–393.
- Krause, J., Ruxton, G. D., & Krause, S. (2010). Swarm intelligence in animals and humans. *Trends in Ecology and Evolution*, *25*(1), 28–34.
- Kudo, H., & Dunbar, R. I. M. (2001). Neocortex size and social network size in primates. *Animal Behaviour*, *62*, 711–722.
- Kusayama, T., Bischof, H. J., & Watanabe, S. (2000). Responses to mirror-image stimulation in jungle crows (*Corvus macrorhynchos*). *Animal Cognition*, *3*, 61–64.
doi:10.1007/s100710050051
- Laland, K. N. (2004). Social learning strategies. *Animal Learning & Behavior*, *32*(1), 4–14. doi:10.3758/BF03196002
- Laland, K. N., & Williams, K. (1998). Social transmission of maladaptive information in the guppy. *Behavioral Ecology*, *9*, 493–499.
- Lefebvre, L. (2012). Primate encephalization. In M. A. Hofman & D. Falk (Eds.), *Evolution of the primate brain: From neuron to behavior* (pp. 393–412). Radarweg, Amsterdam: Elsevier.

- Lefebvre, L., Nicolakakis, N., & Boire, D. (2002). Tools and brains in birds. *Behaviour*, *139*, 939e973.
- Lefebvre, L., Reader, S. M., & Sol, D. (2004). Brains, innovations and evolution in birds and primates. *Brain, Behavior and Evolution*, *63*(4), 233–46.
doi:10.1159/000076784
- Lefebvre, L., & Sol, D. (2008). Brains, lifestyles and cognition: Are there general trends? *Brain, Behavior and Evolution*, *72*(2), 135–144. doi:10.1159/000151473
- Lemaître, J.-F., Ramm, S. A., Barton, R. A., & Stockley, P. (2009). Sperm competition and brain size evolution in mammals. *Journal of Evolutionary Biology*, *22*(11), 2215–2221. doi:10.1111/j.1420-9101.2009.01837.x
- Levenson, R. M., Krupinski, E. A., Navarro, V. M., & Wasserman, E. A. (2015). Pigeons (*Columba livia*) as trainable observers of pathology and radiology breast cancer images. *Plos One*, *10*(11), e0141357. doi:10.1371/journal.pone.0141357
- Maclean, E. L., Hare, B., Nunn, C. L., Addessi, E., Amici, F., Anderson, R. C., ... Zhao, Y. (2014). The evolution of self-control. *Proceedings of the National Academy of Sciences*, *111*(20), E2140–E2148. doi:10.1073/pnas.1323533111
- Macphail, E. M., & Bolhuis, J. J. (2001). The evolution of intelligence: adaptive specializations versus general processes. *Biological Reviews*, *76*, 341–364.

- Magnotti, J. F., Katz, J. S., Wright, A. A., & Kelly, D. M. (2015). Superior abstract-concept learning by Clark's nutcrackers (*Nucifraga columbiana*). *Biology Letters*, *11*, 20150148.
- Magnotti, J. F., Wright, A. A., Leonard, K., Katz, J. S., & Kelly, D. M. (2016). *Abstract-concept learning in black-billed magpies (Pica hudsonia)*. Unpublished manuscript.
- Medina, F. S., Taylor, A. H., Hunt, G. R., & Gray, R. D. (2011). New Caledonian crows' responses to mirrors. *Animal Behaviour*, *82*, 981–993.
doi:10.1016/j.anbehav.2011.07.033
- Menzel, E. W., Jr. (1973). Leadership and communication in young chimpanzees. In E. W. Menzel, Jr. (Ed.), *Precultural primate behavior* (pp. 192-225). Basel, Switzerland: Karger.
- Menzel, E. W., Jr. (1974). A group of young chimpanzees in a one-acre field. In A. M. Schrier & F. Stollnitz (Eds.), *Behavior of nonhuman primates: Modern research trends* (pp. 83-153). New York, NY: Academic Press.
- Mewaldt, L. R. (1948). *Nesting habits and some general notes on Clark's Nutcracker (Nucifraga columbiana Wilson)* (Master's Thesis). Montana State University, Montana.
- Mewaldt, L. R. (1952). The incubation patch of the Clark Nutcracker. *Condor*, *54*, 361.

- Miklósi, Á., Kubinyi, E., Topál, J., Gácsi, M., Virányi, Z., & Csányi, V. (2003). A simple reason for a big difference: Wolves do not look back at humans, but dogs do. *Current Biology, 13*, 763–766. doi:10.1016/S0960-9822(03)00263-X
- Navarrete, A., & Laland, K. (2015). Brain size and innovation in primates. In A. B. Kaufman & J. C. Kaufman (Eds.), *Animal Creativity and Innovation* (pp. 241-285). Cambridge, MA: Academic Press.
- Olson, D. J., Kamil, A. C., Balda, R. P., & Nims, P. J. (1995). Performance of four seed-caching corvid species in operant tests of nonspatial and spatial memory. *Journal of Comparative Psychology, 109*, 173–181. doi:10.1037/0735-7036.109.2.173
- Ostojić, L., Legg, E. W., Shaw, R. C., Cheke, L. G., Mendl, M., & Clayton, N. S. (2014). Can male Eurasian jays disengage from their own current desire to feed the female what she wants? *Biology Letters, 10*(3), 20140042. doi:10.1098/rsbl.2014.0042
- Ostojić, L., Shaw, R. C., Cheke, L. G., & Clayton, N. S. (2013). Evidence suggesting that desire-state attribution may govern food sharing in Eurasian jays. *Proceedings of the National Academy of Sciences of the United States of America, 110*(10), 4123–4128. doi:10.1073/pnas.1209926110
- Overington, S. E., Dubois, F., & Lefebvre, L. (2008). Food unpredictability drives both generalism and social foraging: a game theoretical model. *Behavioral Ecology, 19*(4), 836–841. doi:10.1093/beheco/arn037

- Pérez-Barbería, F. J., Shultz, S., & Dunbar, R. I. M. (2007). Evidence for Coevolution of Sociality and Relative Brain Size in Three Orders of Mammals. *Evolution*, *61*(12), 2811–2821. doi:10.1111/j.1558-5646.2007.00229.x
- Pitnick, S., Jones, K. E., & Wilkinson, G. S. (2006). Mating system and brain size in bats. *Proceedings of the Royal Society B: Biological Sciences*, *273*(1587), 719–724. doi:10.1098/rspb.2005.3367
- Pongrácz, P., Miklósi, A., Kubinyi, E., Topál, J., & Csányi, V. (2003). Interaction between individual experience and social learning in dogs. *Animal Behaviour*, *65*, 595-603.
- Povinelli, D. J., Rulf, A. B., Landau, K. R., & Bierschwale, D. T. (1993). Self-recognition in chimpanzees (*Pan troglodytes*): distribution, ontogeny, and patterns of emergence. *Journal of Comparative Psychology*, *107*, 347–372.
- Prior, H., Schwarz, A., & Güntürkün, O. (2008). Mirror-induced behavior in the magpie (*Pica pica*): Evidence of self-recognition. *PLoS Biol*, *6*(8), 1642. doi:10.1371/journal.pbio.0060202
- Reader, S. M., & Laland, K. N. (2002). Social intelligence, innovation, and enhanced brain size in primates. *Proceedings of the National Academy of Sciences, U.S.A.*, *99*, 4436e4441.

- Rehkämper, G., Frahm, H. D., & Zilles, Z. (1991). Quantitative development of brain and brain structures in birds (Galliformes and Passeriformes) compared to that in mammals (insectivores and primates). *Brain, Behavior and Evolution*, *37*, 125–143.
- Rugani, R., Kelly, D. M., Szelest, I., Regolin, L., & Vallortigara, G. (2010). Is it only humans that count from left to right? *Biology Letters*, *6*, 290-292.
doi:10.1098/rsbl.2009.0960
- 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 Behavior and Evolution*, *71*(3), 200-215.
- Sasaki, T., Granovskiy, B., Mann, R. P., Sumpter, D. J. T., & Pratt, S. C. (2013). Ant colonies outperform individuals when a sensory discrimination task is difficult but not when it is easy. *Proceedings of the National Academy of Sciences*, *110*(34), 13769–13773. doi:10.1073/pnas.1304917110
- Seed, A. M., Tebbich, S., Emery, N. J., & Clayton, N. S. (2006). Investigating physical cognition in rooks, *Corvus frugilegus*. *Current Biology*, *16*, 697–701.
- Seeley, T. D. (2010). *Honeybee democracy*. Princeton, NJ: Princeton University Press.
- Sherry, D. (2005). Do ideas about function help in the study of causation? *Animal Biology*, *55*(4), 441–456. doi:10.1163/157075605774840950

- Sherry, D. F., & Hoshoooley, J. S. (2010). Seasonal hippocampal plasticity in food-storing birds. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 365(1542), 933–943. doi:10.1098/rstb.2009.0220
- Shettleworth, S. J. (2009). *Cognition, evolution, and behavior* (2nd ed.). Oxford, England: Oxford University Press.
- Singer, T., Seymour, B., O’Doherty, J., Stephan, K. E., Dolan, R. J., & Frith, C. D. (2006). Empathic neural responses are modulated by the perceived fairness of others. *Nature*, 439, 466–469.
- Smaers, J. B., Dechmann, D. K. N., Goswami, A., Soligo, C., & Safi, K. (2012). Comparative analyses of evolutionary rates reveal different pathways to encephalization in bats, carnivorans, and primates. *Proceedings of the National Academy of Sciences of the United States of America*, 109(44), 18006-18011.
- Soler, M., Pérez-Contreras, T., & Peralta-Sánchez, J. M. (2014). Mirror-mark tests performed on jackdaws reveal potential methodological problems in the use of stickers in avian mark-test studies. *PloS One*, 9(1), e86193.
doi:10.1371/journal.pone.0086193
- Spada, E. C., Aureli, F., Verbeek, P., & de Waal, F. B. M. (1995). The self as reference point: Can animals do without it? In P. Rochat (Ed.), *The Self in Infancy: Theory and Research* (pp. 193-215). Radarweg, Amsterdam: Elsevier.
- Surowiecki, J. (2005). *The wisdom of crowds*. New York, NY: Random House.

- Swaney, W., Kendal, J. R., Capon, H., Brown, C., & Laland, K. N. (2001). Familiarity facilitates social learning of foraging behaviour in the guppy. *Animal Behaviour*, *62*, 591-598.
- Swift, K. N., & Marzluff, J. M. (2015). Wild American crows gather around their dead to learn about danger. *Animal Behaviour*, *109*, 187–197.
doi:10.1016/j.anbehav.2015.08.021
- 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 of London B: Biological Sciences*, *276*, 247–254.
- Tebbich, S., Seed, A. M., Emery, N. J., & Clayton, N. S. (2007). Non-tool-using rooks, *Corvus frugilegus*, solve the trap-tube problem. *Animal Cognition*, *10*, 225–231.
- Teschke, I., Cartmill, E. a., Stankewitz, S., & Tebbich, S. (2011). Sometimes tool use is not the key: no evidence for cognitive adaptive specializations in tool-using woodpecker finches. *Animal Behaviour*, *82*(5), 945–956.
doi:10.1016/j.anbehav.2011.07.032
- Templeton, J. J., & Giraldeau, L.-A. (1996). Vicarious sampling: The use of personal and public information by starlings foraging in a simple patchy environment. *Behavioral Ecology & Sociobiology*, *38*, 105-113.
- Templeton, J. J., Kamil, A. C., & Balda, R. P. (1999). Sociality and social learning in two species of corvids: The pinyon jay (*Gymnorhinus cyanocephalus*) and the Clark's

nutcracker (*Nucifraga columbiana*). *Journal of Comparative Psychology*, *113*(4), 450–455.

Tomasello, M., Carpenter, M., Call, J., Behne, T., & Moll, H. (2005). Understanding and sharing intentions: the origins of cultural cognition. *Behavioral Brain Sciences*, *28*, 675–735. doi:10.1017/S0140525X05000129

Tomback, D. F. (1977). *The behavioral ecology of the Clark's Nutcracker (Nucifraga columbiana) in the eastern Sierra Nevada*. (Doctoral dissertation). University of California, Santa Barbara.

Tomback, D. F. (1978). Foraging strategies of Clark's Nutcracker. *Living Bird*, *16*, 123–161.

Tomback, D. F. (1998). Clark's Nutcracker (*Nucifraga columbiana*). In A. Poole (Ed.), *The birds of North America online*. Ithaca, NY: Cornell Lab of Ornithology. Retrieved from the Birds of North America online. <http://bna.birds.cornell.edu/bna/species/331>. doi:10.2173/bna.331

Tornick, J. K., Callahan, E. S., & Gibson, B. M. (2015). An investigation of quantity discrimination in Clark's nutcrackers (*Nucifraga columbiana*). *Journal of Comparative Psychology*, *129*(1), 17–25. doi:10.1037/a0037863

Tornick, J. K., & Gibson, B. M. (2013). Tests of inferential reasoning by exclusion in Clark's nutcrackers (*Nucifraga columbiana*). *Animal Cognition*, *16*, 583–597. doi:10.1007/s10071-013-0595-1

- Tornick, J. K., Gibson, B. M., Kispert, D., & Wilkinson, M. (2011). Clark's nutcrackers (*Nucifraga columbiana*) use gestures to identify the location of hidden food. *Animal Cognition*, *14*(1), 117–125. doi:10.1007/s10071-010-0349-2
- Vander Wall, S. B., & Hutchins, H. E. (1983). Dependence of Clark's Nutcracker, *Nucifraga columbiana*, on conifer seeds during postfledging period. *Canadian Field-Naturalist*, *97*, 208-214.
- Vander Wall, S. B., & Jenkins, S. H. (2003). Reciprocal pilferage and the evolution of food-hoarding behavior. *Behavioral Ecology*, *14*(5), 656.
doi:10.1093/beheco/arg064
- Vernouillet, A., Anderson, J., Clary, D., & Kelly, D. M. (in press). Inhibition in Clark's nutcrackers (*Nucifraga columbiana*): results of a detour-reaching test. *Animal Cognition*. doi:10.1007/s10071-016-0952-y
- Ward, A. J. W., Sumpter, D. J. T., Couzin, I. D., Hart, P. J. B., & Krause, J. (2008). Quorum decision- making facilitates information transfer in fish shoals. *Proceedings of the National Academy of Sciences USA*, *105*(19), 6948–6953.
- White, D. J., & Galef, B. G., Jr. (1999). Mate-choice copying and conspecific cueing in Japanese quail, *Coturnix coturnix japonica*. *Animal Behaviour*, *57*, 465-473.
- White, D. J., & Galef, B. G., Jr. (2000). “Culture” in quail: Social influences on mate choices in female *Coturnix japonica*. *Animal Behaviour*, *59*, 975-979.

Whiten, A., & Byrne, R. (1997). *Machiavellian Intelligence II: Extensions and Evaluations*. Cambridge, UK: Cambridge University Press