

Do Birds Have a Theory of Mind?

by

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Author's Declaration

I hereby declare that I am the sole author of this thesis. This is a true copy of the thesis, including any required final revisions, as accepted by my examiners.

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Abstract

It is well known that humans are able to represent the mental states of others. This ability is commonly thought to be unique to humans. However, recent studies on the food caching, gift giving, and cooperative behaviours of Corvids and Parrots provide evidence for this ability in birds. Upon examining the empirical evidence, I argue that the best explanation for these behaviours is that birds are able to represent conspecifics as having particular mental states. I further argue that birds are able to do this by simulating the minds of conspecifics.

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Chapter One: What is a Bird's Theory of Mind?

1.1 Introduction

Traditionally, humans have been the center of discussion when it comes to matters of the mind. Humans employ a number of sophisticated cognitive skills which allow them to interact successfully in highly complex social environments. It is well known that humans are able to represent the mental states of others and use these mental states to predict, understand, and manipulate the behaviour of others with great success. This ability has been given a number of labels including: Theory of Mind (ToM), mindreading, and mentalizing. Though 'ToM' is perhaps the most well-known label for this ability across academic fields, it is also the most ambiguous. I will clear up this ambiguity soon, but for now I will use the term to refer simply to the ability to represent the mental states of others. Though it is obvious that humans have a ToM, it is less obvious whether this ability is unique to humans. Thus far, to the extent that ToM research has been done on non-human animals, much of it has been focused on chimpanzees and the other great apes. This seems like a natural place to look; if any non-human animal were to possess a ToM, then surely it would be one of our closest relatives. However, recent experimental findings have suggested a new animal star in the ToM debate: birds. To most human observers, birds appear to spend the majority of their time making nests, eating worms, and producing the wonderful birdsong that we hear coming from the trees. For some birds this may be an accurate description, but for others, particularly members of the Corvidae (crows and jays) and the Psittaciadae (parrots, cockatoos, and relatives) families, there appears to be more going on between their feathered ears.

The three goals of this paper are to clarify the nature of ToM, specify the best argument for ToM in birds, and to evaluate the plausibility of this argument. In doing this, it is my intention to show that some birds are able to represent conspecifics as having particular mental states that are different from their own and thus have a ToM. I will begin by reviewing the different ways in which the term ‘ToM’ has been used in various fields and clarify how I will be using the term here. I will outline the ToM that I think some birds have and show how this ToM differs from human ToM. In the second chapter, I will examine the empirical evidence and make a case for ToM in birds. In the third chapter, I will address critics who reject the claim that non-human animals *could* have a ToM and show why their objections fail to rule out this possibility. I will also respond to critics who claim that the studies on non-human animals, including birds, do not provide adequate evidence for a ToM.

1.2 What is Theory of Mind?

The term “theory of mind” was first introduced by David Premack and Guy Woodruff in their (1978) paper “Does the Chimpanzee Have a Theory of Mind?” Since then, psychologists have studied the ability to represent a conspecific as having mental states under the label “theory of mind.” I take ToM to be the ability to represent others as having particular mental states that are different from one’s own. However, there are different approaches to ToM, that is, different explanations for this ability, and this is where the ambiguity stems from.

The term “*theory* of mind” seems to imply the use of some kind of theory in representing the mental states of others. Indeed, the Theory-Theory (TT) approach maintains that certain mental capacities, including the capacity to explain and predict a conspecific’s behaviour, are underpinned by a naïve psychological theory. However, TT is just one possible explanation for

the ability to represent the mental states of others. Simulation-Theory (ST) is another possible explanation for the ability to represent the mental states of others. Though the term “simulation-*theory*” may suggest otherwise, ST does not include anything theory-like in its explanation of the ToM ability. As a result of this ambiguity, the terms “mindreading” and “mentalizing,” endorsed by (Nichols & Stich, 2003; Goldman, 2006), have been used to replace the term “ToM” to refer to the ability to represent the mental states of others. These terms, though fairly common in philosophical literature, are not widely used outside of philosophy. The majority of the comparative cognition literature still uses the term “ToM”. From here on, I will use the term “ToM” to mean the ability to represent a conspecific as having a particular mental state that is different from one’s own. To be clear, I do not, by using this term, wish to imply that any sort of psychological theory is necessarily involved in the representing of mental states of others.

1.3 Approaches to Theory of Mind

I have already mentioned that there are different approaches to explaining the ability to represent the mental states of others. In a summary of the ToM debate, Alvin Goldman (2006) distinguishes three unique approaches to mental state representation: Theory-Theory (TT), Rational Theory (RT), and Simulation Theory (ST). I will briefly explain each of these here but focus on ST as this is the approach that is most relevant for explaining ToM in birds. TT, as I have previously explained, says that people use their naïve psychological theory to guide them in representing the mental states of others (Stich & Nichols, 1992). RT says that ordinary people are rational and thus represent the mental states of others in accordance with some rationality postulate (Davidson, 1984; Dennett, 1987). ST says that people represent the mental states of others through simulation; this act of simulation is commonly referred to as “putting oneself in

another's shoes." Alvin Goldman, argues that ST is grounded on the belief that all ordinary human beings are decision makers and thus possess the capabilities necessary for making decisions; they possess their own "decision-making mechanism" (2006, p. 20). According to ST, one takes on the initial state of the target (including all desires, beliefs, and goals of the target) and takes in the input being presented to the target's decision making mechanism, in an effort to replicate the decision making process that the target will experience. During simulation for the purpose of representing the mental states of others, the decision making mechanism of the host is run "off-line" (that is, without acting).

TT, RT, and ST all offer explanations as to how one is able to represent others as having particular mental states. In the next section, I will discuss how these approaches apply to birds.

1.4 What Kind of Theory of Mind Does a Bird Have?

So, what kind of ToM do birds have? TT requires that those representing the mental states of others (the representers) have a naïve psychological theory in order to represent others as having a particular mental state. While it is still a matter of debate whether or not humans have a naïve psychological theory, it seems unreasonable to assume that birds could have such a theory. Though some avian brains have much more cognitive power than the idiom "bird-brain" suggests, it is still far from the cognitive power of the human brain. When compared to alternative approaches to ToM that require less cognitive processing power, TT simply does not seem like a reasonable explanation for ToM in birds. RT presents a similar problem for birds. According to RT, one represents the mental states of others in accordance with some rationality postulate. This assumes a sort of formal reasoning that is certainly beyond the capabilities of the

avian brain. ST is a much more plausible approach to ToM in birds as ST is more economical in that it requires fewer conceptual resources than TT and RT.

Alvin Goldman (2006) distinguished between two types of simulation: theory driven simulation and process driven simulation. In theory driven simulation, the representer wishes to simulate a system which is fundamentally different from itself and so must rely on a theory of the target's decision making mechanism. By contrast, in process driven simulation the representer's system resembles the target's system and so the simulation is run by engaging in shared processes and operations. That is, the representer and the target share the same or highly similar decision making mechanisms and thus, by taking in the input presented to the target, the representer is able to run their own decision making mechanism just as the target would. Process driven simulation is more economical than theory driven simulation as it too (like ST versus TT and RT) requires fewer conceptual resources. Process driven simulation is the kind of simulation that birds are capable of.

I take it that birds have a ToM if and only if they are able to represent a conspecific as having a particular mental state that is different from their own. I argue that birds are able to do this by mentally putting themselves in the position of the target and running their own mental mechanisms with the target's input. That is, I argue that birds have a ToM and that process driven ST is the best explanation for this ability.

1.5 The Differences between Birds and Humans

I take the definition of ToM as the ability to represent others as having a particular mental state that is different from one's own to be the same in both human and non-human animals,

despite possible differences in how mental states may be represented and in what kinds of mental states may be represented. That being said, ToM is an ability that is present in various degrees. An adult human, free from any cognitive impairment, has a sophisticated ToM and is capable of representing many kinds of mental states. Birds, I will argue, have only a basic ToM. Whereas humans are capable of representing the higher order mental states of others (e.g. Mary knows that I believe Phil hates broccoli), birds are only capable of representing the first order mental states of others (e.g. that bird knows where the food is). Furthermore, a human's ToM is not limited to conspecifics in that they are able to represent the mental states of non-humans. For example, if a dog rolls his ball under the couch and then stares at the couch intently perhaps trying to reach the out of sight ball with his paw, a human will represent the dog as having a state of knowledge. Similarly, in a game of chess against a computer opponent, a human may represent the computer as having a goal or desire state. Though representing non-human animals and things as having particular mental states is sometimes simply a matter of convenience, it is clear none the less that humans are able to represent the mental states of things and animals outside of their species. Though I am open to the possibility that birds may be able to represent the mental states of non-conspecifics, I will not be supporting this claim here. When I say that birds are able to represent others as having a mental state, I mean by "others" birds.

There has been much talk about the specific nature of mental representations. Though mental representations are generally described as being multimodal, the extent to which mental representations rely on language is still a matter of debate. Though humans may have linguistic representations we have no reason to believe that birds have linguistic representations as we have no reason to believe that birds have language. We still, however, have reason to believe that birds have representations; these reasons will be discussed in chapter two. In humans, mental

representations can be composed of various types of sensory information. Birds and humans share the same five basic senses: sight, hearing, smell, taste, and touch. It is reasonable then to assume that a bird's representations consist of different kinds of perceptual input, though it is likely some senses play larger roles than others.

Finally, I will not take a stand on the best approach to ToM in humans. I have already said that ST is the best approach to ToM in birds. This does not however, mean that I believe that ST captures the whole story when it comes to ToM in all animals. Whatever kind of ToM humans have, it is far more complex than the ToM that birds have. Goldman (2006) argued that what humans have is actually a hybrid theory that includes elements of TT and ST, with an emphasis on simulation. Furthermore, humans may be capable of both theory driven ST and process driven ST, though I argue that birds are only capable of the latter.

1.6 Is Theory of Mind in Birds Even Possible?

For birds, the ability to represent conspecifics as having particular mental states is useful for at least two reasons: it allows the representer to predict the behaviour of conspecifics, and it allows the representer to act according to the mental states of conspecifics and their predicted behaviour. Being able to do both of these things will increase a bird's chances for both survival and success.

The social brain hypothesis points out a relationship between social groups in primates and cognitive processing power (Dunbar, 1998). It implies that larger brain size is selected for in primates because it facilitates complex social interactions; the larger the information processing capacity of a primate, the larger the social groups formed by that primate. A second relevant relationship between neocortex size and social group size has been found; the larger the

neocortex, the larger the social group (Stephan, Frahm, & Baron, 1981). The implications of these relationships are relevant to birds for two reasons. First, birds are highly social animals. Not only do these birds interact with their conspecifics, they do so within complex hierarchical social systems. The fact that these birds are able to maintain many social relationships suggests, by the social brain hypothesis, that they have a high capacity for information processing. The fact that birds have a high capacity for information processing is important for simulation and the representation of the mental states of other birds because doing so requires more cognitive resources than other, simpler cognitive tasks. Second, though birds do not have a neocortex as it is found in the mammalian brain, homologs of the layer 4 input and layer 5 output neurons of the neocortex have been discovered in a part of the avian brain called the ‘dorsal ventricular ridge’ (DVR) (Dugas-Ford, Rowell, & Ragsdale, 2012). In humans, many of the cognitive skills traditionally considered unique to humans are made possible by the neocortex. Without a neocortex, it may seem like an impressive cognitive ability such as ToM would be impossible. However, it seems plausible that the neocortex homolog in birds, the DVR, could be the centre for ToM in birds. Furthermore, birds, like primates, have large brain to body size ratios. So, despite the absence of the neocortex in the avian brain, the presence of homologies in the DVR and a large brain to body size ratio provide birds with the cognitive processing power necessary for ToM. Thus, it is not only the case that we do not have any biological reasons for rejecting the possibility of ToM in birds, the social brain hypothesis along with recent research on the DVR in birds actually provide good reason to believe that ToM in birds is possible.

Chapter 2: Evidence for ToM in Birds

Members of the Corvid and Parrot families are more intelligent than anyone ever expected a bird could be and are highly social. These birds must survive within large social groups and so any strategy that allows a bird to outcompete its conspecific is valuable. In this chapter I will examine the empirical evidence for ToM in birds. I will outline each type of evidence and explain why these behaviours in birds are best explained by the ability to represent conspecifics as having particular mental states.

2.1 Food Caching in Western Scrub-Jays and Ravens

Many animals cache food so that it may be retrieved at a later time (Vander Wall, 1990). To survive, some birds must successfully store food during times of abundance for future consumption when there is a shortage of food. Birds that are more successful at storing food and preventing pilferage are more likely to survive. One potential threat to a bird's caches is a pilfering conspecific. Birds that are able to employ strategies for protecting their caches are more likely to cache food successfully. Caching food for future consumption requires the caching animal to have a well-functioning observational spatial memory so that they may be able to recover their caches successfully and efficiently, (Clayton, Griffiths, Emery, & Dickinson, 2001). As some of these food caching animals are also food cache thieves, in order to cache food successfully, animals must also have strategies for reducing the probability that their caches will be pilfered. The Western Scrub-Jay and to a lesser extent the Raven have been the subjects of a number of experiments focused on food caching behaviour in birds. Not only do these birds cache food items, but they also recache items. These experiments highlight the different kinds of strategies employed by the birds for reducing the chance that their food caches will be stolen.

Recaching is one kind of strategy employed by birds, particularly of lower status. Dominant birds may not need to recache their food items because they are able to defend their caches aggressively. However, for birds that cannot effectively defend their caches aggressively, moving their caches to new locations provides a good strategy for reducing the probability that their caches will be stolen (Dally, Emery, & Clayton, 2005b; Heinrich, 1999). Many of these experiments, and the ones on which I will focus, highlight the social aspects of the birds' food caching behaviours. I will spend the rest of this section reviewing some of the key experiments on food caching behaviours in Western Scrub-Jays and Ravens and then arguing that these behaviours are best explained by ToM.

2.1.1 The Effect of Observation

Matthew Emery and Nicola Clayton designed an experiment to test the effect of observation by a conspecific on the caching behaviours of Western Scrub-Jays (Emery & Clayton, 2001). In the experiment, jays were allowed to cache food items in a sand filled tray in one of two conditions: while being observed by a conspecific (observed condition) or while in private (private condition). After the caching phase, the jays were allowed to recover their caches, always in private, during a recovery phase. The results showed that the jays from the observed condition, recached significantly more food items than the jays from the private condition. The results also showed that the jays from the observed condition preferentially recached in new sites, whereas the jays from the private condition showed no preference between new and old sites.

In order to test the hypothesis that the jays were recaching as a result of the presence of a conspecific during the previous phase, Emery & Clayton did another series of trials in which the

jays completed two caching phases (one private and one observed). The order of the private and observed caching phases was varied, and different trays were used for each caching phase. During the recovery phase (again always in private), the jays were presented with three trays: the tray from the private caching phase, the tray from the observed caching phase, and a new tray. The results of this series of trials showed that the jays recached significantly more items from the observed tray than from the private tray. Furthermore, the items recached from the observed tray were recached preferentially in new sites. The few items that were recached from the private tray were recached indiscriminately. If this caching behaviour were merely triggered by the presence of a conspecific during the caching phase then we would expect to see recaching happening at the same rate in all trays. As the rate of recaching was not the same for all trays, these results show that caching behaviour of the jays is not likely to be triggered by the mere presence of a conspecific during the previous phase.

Thom & Clayton (2013), in response to critics (Van der Vaart, Verbrugge, & Hemelrijk, 2012), also designed an experiment to test the hypothesis that the jays' caching behaviours were the result of stress. Van der Vaart, Verbrugge, & Hemelrijk argue that recaching is a behaviour driven by a desire to cache more rather than a desire to protect existing caches. This desire to cache more is in turn driven by the stress brought on by the presence and dominance of observing conspecifics and failed recovery attempts. Thom & Clayton manipulated the recovery success rate of the birds by stealing some of their caches in order to induce stress and found no evidence that recovery failures result in more caching. Furthermore, Thom & Clayton found that not only did recovery failures fail to result in more caching, recover failures did result in the avoidance of previously pilfered sites by cachers. Thom & Clayton confidently conclude that recaching behaviours in Western Scrub-Jays cannot be attributed to stress.

A more likely explanation for this caching behaviour is that the caching birds are representing the observing conspecifics as having knowledge states. That is, the cacher is representing the observer as having knowledge of cache location. I will quickly note that whether these states count as 'knowledge' by any particular epistemological definition is not my concern here; my only concern is that they are mental states (knowledge or not). I use the term 'knowledge' here for ease of discussion. Now, it is not the case that the cacher is simply representing the observer as having the same knowledge states as itself. If this were true, then the cacher should recache an equal number of items from the private tray and the observed tray since the cacher has knowledge of cache locations in both trays. The fact that the cacher recaches significantly more items from the observed tray than the private tray suggests that the cacher is able to distinguish between its own knowledge states and the knowledge states of the observer. By mentally putting itself in the position of the observing conspecific, the cacher is able to run its own decision making mechanism and based on the perceptual input available to the observer represent the knowledge states of the observing conspecific. Through this simulation the cacher also represents the observer's intention to pilfer the caches. With the representations of the observer's knowledge states and intentions, the cacher decides, through the normal running of its own decision making mechanism, to recache the vulnerable food items.

During the experiment, Emery & Clayton discovered that it was only the jays that had previous experience with pilfering who exhibited these patterns in recaching behaviour. Furthermore, Emery & Clayton discovered that it was previous experience as a pilferer, and not previous experience as an observer, that was crucial. With these findings, Emery & Clayton concluded that this experiment demonstrates that jays can remember the social context of specific past events, and adjust their present behaviour so as to avoid potentially detrimental

consequences in the future (such as their food caches being pilfered). As previous experience as a thief is crucial to this behaviour, Emery & Clayton argue that the jays project their experience as a pilferer to their current situation in which their own caches may be pilfered. Emery & Clayton suggest that this may be a good candidate for understanding the knowledge states of conspecifics and the use of knowledge to influence behaviour and plan for the future. Though they do not outright claim that this is evidence for ToM in birds at this point, in a later publication, Emery and Clayton say that:

“These results suggest that the jays understood that the observer knew the location of their caches, and therefore when they return to the cache sites, they should protect them by moving them to new places, whereas if the bird could not observe them during caching because their view was blocked (in-private condition), they would be ignorant of the caches’ location and so recaching would not be required,” (Emery & Clayton, 2009, p. 99).

From a ToM perspective, it is easy to see why this past experience as a thief is so important. When cachers represent the mental states of other birds, they do so through process driven simulation. The cacher mentally puts itself in the position of the observer and uses the input available to the observer to run its decision making mechanism on behalf of the observer. For birds with past thieving experience, the decision or intention to steal a cached food item happens when knowledge of a cache location becomes available. However, if a bird does not possess past thieving experience then, when its decision making mechanism is run, it will not generate the intention to pilfer cached food items, and so it is not able to represent a conspecific as having that mental state. Similar examples involving paired deficits can be seen in humans. In paired deficit cases, there is a deficit in the subject’s *experience* of particular emotion as well as a deficit in the subject’s *recognition* of that same emotion (see Adolphs, Tranel, Damasio, & Damasio, 1994; Sprengelmeyer, et al., 1999). Goldman (2006) noted that these types of deficits are predicted and easily explained by process driven ST. The lack of thieving experience,

though not the result of a brain injury as in some human paired deficit cases, causes a similar type of problem when using a ToM: a representer's inability to experience a particular emotion or mental state prevents them from representing that same emotion or mental state in others. In the case where a jay lacks previous experience as a thief, the jay's inability to produce the intent to pilfer through their own mental mechanisms prevents the jay from being able to represent a conspecific's intent to pilfer through simulation. By contrast, jays with past experience as a thief are able to produce the intent to pilfer through their own mental mechanisms and so are able to represent the intent to pilfer in others through simulation.

Though it is easy to see how caching behaviours may be explained in terms of ToM, there are still alternative explanations for how birds employ these cache protection strategies. For instance, the birds could be reacting to behavioural cues from observing conspecifics, they could be reacting to stress, they could be attributing their own knowledge states to conspecifics, or they could be exhibiting learned (associative) behavior. Each of these alternative explanations has been addressed and tested for in an experimental setting. I will continue to examine cache protection strategies employed by birds and will also consider alternative explanations for the remainder of section 2.1.

2.1.2 The Effect of Lighting

Dally, Emery, & Clayton (2004) published an experiment that was designed to test whether or not Western Scrub-Jays could exploit an environmental variable, the amount of ambient lighting, in order to decrease the chance that their food caches would be stolen. In the experiment, the jays were allowed to cache non-degradable food items in two separate trays. One tray was well lit while the other tray was in shadow. The jays were allowed to cache in two

possible conditions: in private (private condition), or while being observed by a conspecific (observed condition). The results showed that jays in the private condition had no preference between the well-lit tray and the shaded tray, and cached in each tray equally. Jays from the observed condition cached preferentially in the shaded tray. The hypothesis was that by caching in the shaded tray, the quality of the observer's visual information on the caching would be reduced, thus making the location of the cache more difficult to determine. Dally et al. concluded that Western Scrub-Jays selectively cache in shaded locations as a strategy for preventing pilferage by observing conspecifics.

The best explanation for this cache protection strategy is ToM in birds. In this experiment, the birds were not given a chance to recache their food items in a recovery phase; in any case, even if the birds were going to be given a chance to recache, they would not have known this ahead of time. During the caching phase, the cacher simulates the observer's mental mechanism in order to represent the observer's knowledge of cache location, which in turn leads to the representation of the observer's intention to pilfer the caches. By caching food items in the shaded tray versus the well-lit tray, the cacher is able to reduce the amount of information (in this case visual information) available to the observer, thus reducing (or degrading) the observer's knowledge of cache locations.

The preference for caching in the shaded tray cannot simply be explained by an aversion to the light source, as the jays cached equally in the shaded and well-lit trays during the private condition. This experiment also tested for the possibility that the cacher was simply representing the observer as having the same knowledge states as itself. If the cacher were simply representing its own knowledge states in the observer, then we would not expect to see a

preference for caching in one tray over another, since the cacher's knowledge of cache location is unaffected by the visibility of the tray.

2.1.3 The Effect of Distance and the Observer's Position

In a similar study done by Dally et al. (Dally, Emery, & Clayton, 2005a), three experiments were done in which Western Scrub-Jays were allowed to cache food items in two different locations and the position of the observing conspecific varied. The jays were later allowed to recover their caches, always in private.

In the first experiment, one tray was placed near the observer and one tray was placed farther away from the observer, see figure 1. In one set of trials the jays cached in private (private condition), and in another set of trials the jays cached while being observed by a conspecific (observed condition). There were a number of interesting results from the first experiment. First, the jays preferentially cached in the far tray in the observed condition, but showed no preference in the private condition. Second, jays in the observed condition cached significantly more items than jays in the private condition. Third, during the recovery phase, the jays from the observed condition recached significantly more items (as a proportion of the total items cached) than the jays from the private condition. Fourth, during the recovery phase, jays from the observed condition recached a significantly higher proportion of food items from the near tray than from the far tray. In contrast, jays from the private condition showed no statistically significant difference in the proportion of food items that were recached from either the near or far tray. Fifth, when jays recached their food items, they could be placed in new or old sites. Jays from the private condition recached in new and old sites equally, whereas jays from the observed condition recached exclusively in new sites.

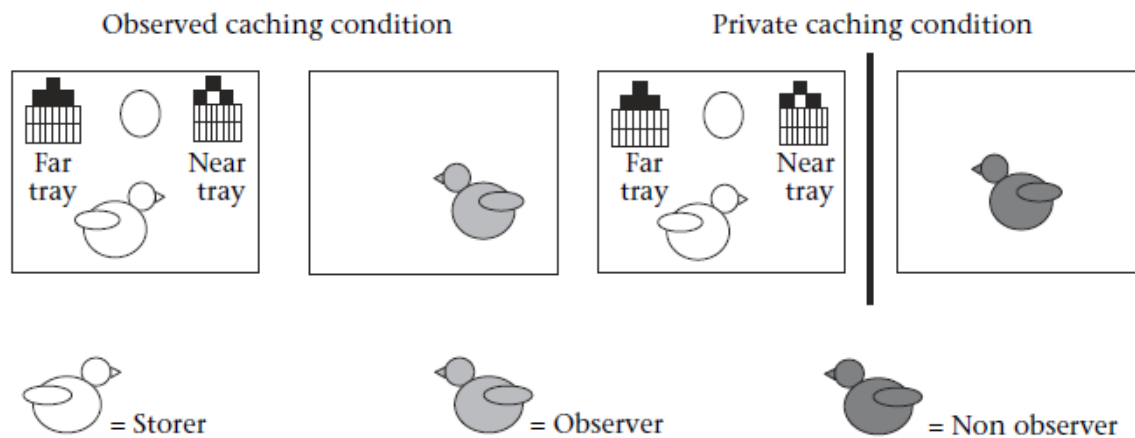


Figure 1: Experiment 1 set up from Dally et al. 2005a

From this first experiment, Dally et al. concluded that jays use relative distance from conspecifics as a way to reduce the amount of information about the caching that the observer has, thus decreasing the chance that their caches will be pilfered. The higher rate of caching in the observed condition led Dally et al. to conclude that the jays were compensating for the presence of a conspecific by hiding more food items than in the private condition. They also observed that jays do significantly more recaching after being observed by a conspecific, and that the jays preferentially recached those items that were at the highest risk of being stolen due to their locations being nearest to the observer.

These results are all easily explained by ToM in birds. If a cacher is representing an observing conspecific as having knowledge of cache locations and that knowledge makes the observer a threat as a potential pilferer, it makes sense for the cacher to attempt to reduce the amount of knowledge that the observer has. In the observed condition, jays attempted to reduce the amount of visual information available to the observer by preferentially caching in the tray that was farther from and thus less visible to the observer. In the private condition, the jays had no motivation for caching in the far tray as opposed to the near tray and showed no preference

when caching. As Dally et al. suggest, the increase in the number of items cached in the observed condition versus the private condition can be viewed simply as a sort of insurance policy against pilferage; the more items a bird has cached, the greater the chance some items will be left after pilferage occurs. As we saw in 2.1.1, recaching food items also allows the cacher to reduce the knowledge of the observer by moving items from locations that the observer witnessed items being cached at, to locations that the observe did not witness items being cached at. Not only did the jays from the observed condition recache significantly more items (as a proportion of the total items cached) than the jays from the private condition during the recovery phase, but they also recached a significantly higher proportion of food items from the near tray than from the far tray. The items located in the near tray were more visible to the observer and thus more known to the observer and so were preferentially recached. Another strategy for reducing the observer's knowledge of cache location was the preference to cache in new locations as opposed to old locations. If a cacher recaches a food item in an old location (a location which previously contained a food item), then it has not done anything to reduce the observer's knowledge of the food item's location since the observer still believes that there is a food item at that location. The fact that cachers in the observed condition preferentially recached in new locations, shows that the recaching strategy is informed by the observing conspecific's knowledge states.

In the second experiment, jays were again allowed to cache food items in two separate trays, in one of two conditions. In the first condition (the free condition), an observing conspecific was able to freely move about an enclosure and view either of the trays, but could not simultaneously view both trays due to an obstructing barrier, see figure 2a. This meant that

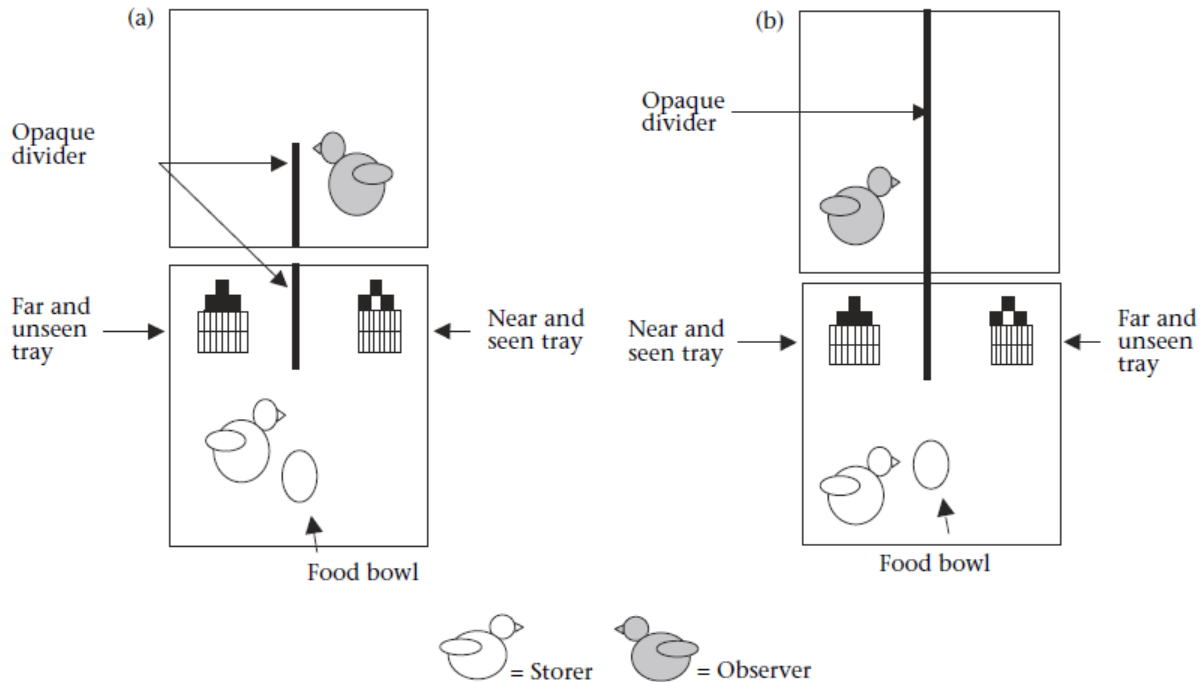


Figure 2: Experiment 2 set up from Dally et al. 2005a

one tray was ‘near and seen’ and one tray was ‘far and unseen’ but which tray was which was determined by the location of the freely moving observing conspecific. In the second condition (the constrained condition), the observing conspecific was constrained to one side of the enclosure and could only ever view one of the two trays, see figure 2b. This meant that one tray was always ‘near and seen’ and the other tray was always ‘far and unseen’. Again the jays were later allowed to recover their caches, always in private.

The results of this second experiment showed that jays from both the free and constrained conditions preferred to cache in the far and unseen sites. They also showed that during the initial caching phase, jays would move items that were cached in view of a conspecific around multiple times before finally depositing them in one location. Both jays from the free condition and the

constrained condition exhibited this behaviour, but it was much more frequent in the jays from the free condition.

In order to test the hypothesis that the jays were avoiding the area of the cage closest to the observing conspecific and therefore preferentially caching farther from the observer due to fear of the open or of the conspecific, a set of control trials were done in which the jays were given powdered (therefore non-cacheable) food and watched to see how much time they spent in each area of the cage. The results of the control trials showed that the jays spent an equal amount of time in all areas of the cage and thus did not preferentially cache in a particular tray as a result of an aversion to open areas or areas near the observing conspecific.

From the second experiment, Dally et al. reconfirmed their conclusion from the first experiment, and also went on to suggest that a second cache protection strategy had been employed as a result of the uncertainty in the observer's position: moving items around multiple times before finally depositing them in a location. In the free condition, where this behaviour was much more frequent, the observing conspecific's location was uncertain. Dally et al. explain that, presumably, the motivation for repeatedly moving caches in the presence of a conspecific is different than the motivation for recaching items in private during the recovery phase. When jays recached their food items in private, they moved the food items from the locations in which the items were hid when the conspecific was in view, to locations that were not seen by the observing conspecific to contain food items (Emery & Clayton, 2001). Dally et al. suggest that when jays move items around multiple times in the presence of the observing conspecific, it is likely in order to confuse observers of the actual location of the cached food item. This is similar to the technique used by magicians to confuse audience members of the location of a ball hidden under a cup. The magician quickly moves the ball between cups while at the same time rapidly

changing the order of the cups. The magician's strategy makes it significantly more difficult for an audience to accurately keep track of the location of the ball.

Again, this is an attempt to interfere with the observer's knowledge states. Cachers make many false caches (caches where a bill probe into the sand is made but no food item is deposited) before finally depositing a food item in a location so as to confuse observers of the real location of the food item. In order to reduce the chances that the observer will be successful in its pilfering, the cacher attempts to confuse the observer by making the false caches. This can be seen as a form of deception since the cacher physically goes through the motions of making a cache, without actually depositing a food item, in an attempt to make the observer believe that a food item is cached at a location where it is actually not.

In the third experiment, jays were again allowed to cache food items in two separate trays, in one of two conditions: private or observed. This experiment was designed to test whether the jays would preferentially cache in sites unseen by the observer, when distance was removed as a protection strategy. In this experiment, one tray was located "in-view" of the observer and the other tray was located "out-of-view" of the observer, but both trays were equidistant from the observer, see figure 3. As in the second experiment, a series of control trials were conducted in order to rule out the possibility that the jays were preferentially caching out of view of the conspecific observer due to fear of the open or the presence of the conspecific. Again, the results of the control trial showed that the jays spent an equal amount of time in all areas of the cage, and so were not caching preferentially due to an aversion to the open or to the observing conspecific. The results from the third experiment showed that jays in the observed condition cached preferentially in the out-of-view tray, and the jays in the private condition

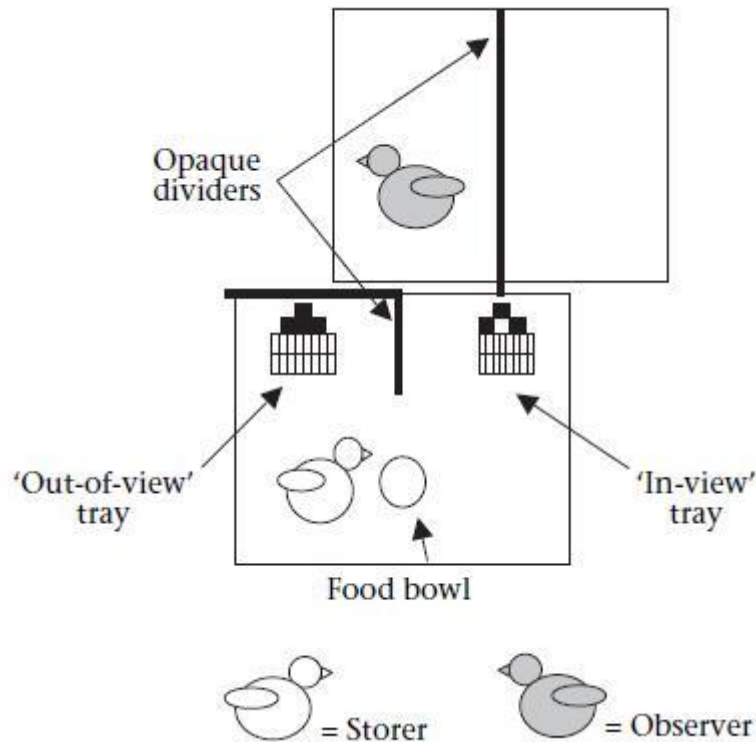


Figure 3: Experiment 3 set up from Dally et al. 2005a

showed no preference and cached equally in both trays. Results also showed that the jays moved few items around during the caching phase, similar to the constrained condition in the second experiment. The few items that were moved around were moved from both the in-view and out-of-view trays equally.

From the third experiment, Dally et al. concluded that jays preferentially cached in unseen sites, even when distance was not a factor. They further suggested that since the jays did not move cached food items around as frequently as they did in experiment two, the consistency of the observer's position reduced the need for a confusion tactic.

Dally et al. were careful to note alternative explanations that were tested for in the experiments. Preference for caching in out-of-view trays is unlikely to be a result of differential

reinforcement as only a single trial was completed for each experiment by any particular bird. Preference for caching in out-of-view trays is also unlikely to be a result of preference for solitude as control trials showed that the jays spent an equal amount of time in all areas of the cage. Dally et al. also found that caching patterns were not related to a preference for avoiding conspecifics as the rate of caching was the same for private and observed conditions. The results of the third experiment showed that caching strategies could not be attributed to a distance strategy as both trays were equidistant from the observer. That is, the caching patterns exhibited by the birds could not simply be explained by an association between the presence of an observer and caching in a farther tray because the caching patterns were still exhibited even when distance was removed as a factor.

In all three experiments, jays did cache some food items in non-preferred sites (that is, near or in-view). During the recovery phase, jays selectively recached these high risk items to new locations. Dally et al. suggest that this may be just another strategy for preventing pilferage, because hiding all caches in the same area may become predictable and thus easier to steal. Dally et al.'s general conclusion was that jays use multiple strategies in order to prevent pilferage of their food caches. These strategies include maximizing the distance between the cache location and the observer so as to decrease the visual information gained by the observer, increasing the total number of items cached when being observed, moving items around multiple times in an attempt to confuse the observer about the actual locations of the food items, and selectively recaching high risk items. Though Dally et al. are cautious in their conclusion, they do claim that these results suggest that jays are capable of complex social cognition. They further claim that these results, along with other evidence, provide evidence for the ability to represent conspecifics as having particular mental states.

2.1.4 The Effect of Multiple Observers

Further studies on the effects of observation on food caching behaviour (Dally, Emery, & Clayton, 2006; Emery & Clayton, 2001) showed that jays are able to recognize the different knowledge states of particular observers. In these studies a cacher was allowed to hide food in tray A in the presence of an observer A while a second tray B was present but covered so that the cacher was unable to hide food in tray B. After hiding the food in the presence of observer A, observer A was then removed and observer B became present. At the same time, tray A was covered and tray B was uncovered. The cacher was now allowed to hide new food items in the presence of observer B. Three hours after all the initial caching was done, the cacher was allowed to return to trays A and B and was given the opportunity to recache their initial food caches in one of four conditions: in the presence of observer A, in the presence of observer B, in the presence of a naïve bird (observer C) that was not present during any of the original caching, or in private. The results showed that the birds preferentially recovered the caches that the present observer had seen them make during the time of the initial caching. That is, in condition one where observer A was present during the recovery phase, the cacher selectively recached the food items from tray A (the tray that observer A viewed during the initial caching phase). In condition two where observer B was present, the cacher selectively recached the food items from tray B. In condition three, where a naïve bird (Observer C) was present, the cacher recached no food items. In condition four, the private condition, the cacher recached food items from both trays A and B.

These results show that the jays are sensitive to the different knowledge states of different observers. That is, the birds realize that although they should move their caches which are at locations known to the observer, their recaching should also not result in any new information

being given away to particular observers. As in the case where only one observer was present, cachers mentally put themselves in the position of the observing conspecific and simulate the observer's mental mechanism. The difference in this experiment is that the cachers simulated multiple observers on an individual basis. The cacher had not just one representation of the mental state of all observers, but the cacher had a unique representation for the mental state of each observer. Cachers also appeared to deceive observers by moving recached food items up to six times and by sometimes leaving the food items in an earlier location while continuing to make bill probes as they would if they were caching a food item (false caches) (Dally, Emery, & Clayton, 2006).

To further support this conclusion Dally et al. designed a control experiment in order to test the hypothesis that the caching jays were simply reading the behavioural cues of the observing conspecific. In this control experiment, a cacher was allowed to cache in two trays (A and B) while being observed by a conspecific, but could only cache in tray A in the presence of observer A, and could only cache in tray B in the presence of observer B. After the original cacher had cached in both trays A and B, the trays were removed and presented to a second cacher (C), who was allowed to cache in both trays while being observed by a new observer (D). Later, during the recovery phase, both trays A and B were returned to the original cacher in the presence of observer D. Dally et al. hypothesized that if caching birds were simply reacting to behavioural cues produced by an observing conspecific, then the cacher should react to the behavioural cues regardless of whether or not the observer was present during that particular cacher's caching phase. In this experiment, if the original cacher was simply reacting to behavioural cues from an observer, then when observer D is present for the recovery phase, the original cacher should recache equally from both trays as observer D witnessed caching in both

trays (although by a different cacher, C). By contrast, if cachers are representing the mental states (in this case knowledge states) of observing conspecifics, then cachers should only recache from the trays observed by the observer present during the recovery phase. The results of this control experiment showed that this is indeed what the cachers did. Cachers successfully represented and kept track of the unique knowledge states of different observing conspecifics. When observer D was present during the recovery phase, the original cacher did not recache items from either tray, similar to the recovery phase where a naïve bird was present in the previous experiment. Based on these results, Dally et al. concluded that it is unlikely that patterns in recaching behaviour can be attributed simply to the reading of behavioural cues produced by observing conspecifics.

2.1.5 Ravens

Though many of the food caching studies have featured Western Scrub-Jays as the subjects of interest, the food caching behaviour of Ravens has also been studied in a more naturalistic environment (Heinrich, 1999). Heinrich made many observations about the caching behaviours of Ravens that supported the findings in Western Scrub-Jays that cachers are sensitive to the different knowledge states of observers. Just as the Western Scrub-Jays in Dally et al. 2005a, Ravens appear to choose cache sites that are out of view and as far as possible from potential pilferers (Bugnyar & Kotrschal, 2002; Heinrich, 1999). Bugnyar & Kotrschal (2002) also suggest that Ravens are capable of tactical deception as they appear to be able to withhold information about their intentions in both caching and pilfering roles and can therefore manipulate the attention of their conspecifics. Bugnyar also got results that supported the claim that Ravens can tell the difference between knowledgeable and naïve birds (2007).

Though the studies done with Ravens are important for showing that these food caching behaviours are not unique to Western Scrub-Jays and for providing further evidence of ToM in birds, unfortunately not all of these studies were done in strict experimental settings. For this reason, though these behaviours in Ravens are easily explained by the representation of the mental states of conspecifics, just as they are in Western Scrub-Jays, we must be cautious of alternative explanations that were not tested for in these experiments.

2.1.6 Food Caching in Western Scrub-Jays Conclusion

Emery & Clayton (2009) noted that there are three potential explanations for the results of the food caching studies: a low-level explanation, a mid-level explanation, and a high-level explanation. The low-level explanation is based on associative learning and suggests that caching birds associate specific caching events with the presence or absence of a specific observing conspecific. Emery & Clayton note that this low-level explanation may be able to explain the caching behaviour in the studied birds but argue that it would need to be more sophisticated and allow for the integration of past information (social context during caching) with future planning (potential pilfering by the observing conspecific). Emery & Clayton also note that the effects of learning had also been reduced in their studies on Western Scrub-Jays by limiting the number of caching and recovery phases to one.

The mid-level explanation is based on behaviour-reading without an understanding of a conspecific's mental states. This mid-level explanation suggests that observing conspecifics produce behavioural cues, such as directed attention or prolonged attention, that non-observing conspecifics do not produce and that cachers 'read' these behavioural cues and act accordingly. However, based on the results of the control experiment done in Dally et al. 2006 (discussed in

section 2.1.4) it seems unlikely that the recaching behaviour of the birds can be explained by simple behaviour reading.

The third, high-level, explanation suggests that cachers understand and represent the mental states of others (e.g. knowledge of cache location). It also suggests that cachers can remember which conspecifics were watching when, and therefore represent the different mental states (e.g. knowledge and ignorance) of individuals based on their presence or absence during caching. The results from Emery & Clayton 2001, which showed that previous experience as a thief is necessary for the ability to employ these cache protection strategies led Clayton et al. to suggest that experience projection is responsible for the ability to represent the mental states of conspecifics (Clayton, Dally, & Emery, 2007; Emery & Clayton, 2004; Emery & Clayton, 2008). Though Clayton et al. did not go into the details of the simulation they call “experience projection,” I take this to be the same kind of simulation that Goldman (2006) refers to as ‘process driven’ simulation.

By manipulating experimental structure, alternative explanations for the behaviours of these birds have been tested. The results show that it is unlikely that the birds are reacting to behavioural cues from conspecifics, reacting to stress, attributing their own knowledge states to conspecifics, or exhibiting learned (associative) behavior. If these patterns in recaching behaviour had a behavioural explanation, then we would expect to see this behaviour in all birds that cache while being observed. However, as Emery & Clayton found, it is only the birds that have had previous experience as a pilferer who exhibit these recaching strategies. In an interview with The Science Network, Clayton remarked that “...it takes a thief to know a thief” (Interview with Nicola Clayton, 2010) and by explaining these caching patterns in terms of ToM made possible by process driven simulation, we can easily see why.

All of these food caching behaviour experiments provide good evidence for the ability to represent the mental states of conspecifics in birds. By representing the mental states of conspecifics, such as knowledge or the intention to pilfer, birds are able to employ strategies to reduce the chances that their caches will be pilfered, therefore increasing their chances for survival. One strategy is to reduce the amount of visual information available to observing conspecifics by choosing caching locations which are further away from the observer, in shadowed areas, or behind obstructing barriers. Another strategy employed by cachers involves deceiving or confusing their observing conspecifics by moving cached items around repeatedly, and by making false caches. A third strategy used by cachers to reduce the chances that their caches will be pilfered is to focus their recaching on the items which are at the highest risk of being pilfered. All of these strategies are made possible by a bird's ToM. With the alternative explanations that the birds are reacting to behavioural cues from conspecifics, reacting to stress, attributing their own knowledge states to conspecifics, or exhibiting learned (associative) behavior found to be unlikely, the hypothesis that these caching behaviours are a result of a bird's ability to represent the mental states of other birds is the best explanation. In sections 2.2 and 2.3 I will examine two other types of behaviour that also provide evidence for ToM in birds.

2.2 Food Sharing in Eurasian Jays

In order to survive as a species, individuals within that species must successfully reproduce. For many species, in order to reproduce successfully males must make themselves attractive to females. For Eurasian Jays, part of being an attractive male means giving

appropriate gifts to female mates. If a male jay can represent the desire states of a female partner, the male will be able to give preferred gifts and will therefore increase his attractiveness.

Male Eurasian Jays commonly give food items as gifts to their female partners. In a 2013 study, Ostoji, Shaw, Cheke, & Clayton investigated whether male Eurasian Jays could represent the desire states of their female partners, in order to flexibly feed their mates. In this study, which consisted of three experiments, the desires of the female Eurasian Jays were manipulated by satiating the jays on a particular type of food item, thus leading to a preference to eat something new (Dickinson & Balleine, 1995; Balleine & Dickinson, 1998; Correia, Dickinson, & Clayton, 2007). Specific satiety was important for this study because it allows for a reduced desire in a particular food item, without also necessarily reducing desire for other food items. For example, if you eat pizza for lunch, though you will still be hungry at dinner time, you may prefer to eat something new you have just eaten pizza not too long ago.

In the first experiment, both male and female Eurasian Jays were pre-fed one of three food types: maintenance diet (MD), wax moth larvae (W), or mealworm larvae (M). The jays were then presented with two bowls of food (one M and one W) and allowed to eat freely, while researchers recorded the amount of each food type consumed. Each jay completed three separate trials, each time pre-feeding on a different food type. In order to account for variation in individual food preference, independent of specific satiety, the amount of M and W consumed in the test phases (pre-fed M or W) by each jay were compared to that amounts consumed during that jay's specific baseline (pre-fed MD). The hypothesis was that if the jays were pre-fed a particular food type, then they would become specifically satiated with respect to that food type and therefore eat more of the other food type. The results of this experiment confirmed that all

jays (male and female) developed specific satiety, and upon being pre-fed one particular food type (either M or W), would prefer the non-pre-fed food type when allowed to eat freely.

In the second experiment, male jays were allowed to watch their female partners being pre-fed (seen condition) on one of two kinds of food items: wax moth larvae (W) or mealworm larvae (M). The females were pre-fed in order to achieve specific satiety with respect to either W or M. The males were then given the opportunity to choose, from a single W or M, a food item to give to their female mate. Each male jay was allowed to make this decision twenty times. The hypothesis was that if a male jay watched his mate being pre-fed, then he should adjust his food-sharing behaviour in accordance with his female's specific satiety. In order to prevent the male's own food preferences from governing his behaviour, the male jay was fed a maintenance diet (MD).

The results of this study showed that male jays responded to the current desire state of their female partner and shared less of the food type that the females had been pre-fed. However, these results alone do not show that the male jays were representing the desire states of their females, as their choice in which food type to share could have still been determined by behavioural cues given by the female. In order to test this alternative hypothesis, a second condition was created (unseen condition), in which the male jays were not allowed to watch their female partners being pre-fed. This time, the hypothesis was that if male jays were simply reading the behavioural cues of their females, then the males should still be able to share food according to their females' desires. The results suggested that this hypothesis should be rejected as the males who had not watched their females being pre-fed, did not deliver less of the pre-fed food type to their females. The results showed that males in the unseen condition, unlike the

males in the seen condition, were unable to share food in accordance with their females' desire states.

A similar worry may be that the period of time during which the males were allowed to observe their female partners being pre-fed in the seen condition and not in the unseen condition, gave the male an opportunity to become 'better' at reading their females' behavioural cues. However, this study used male-female pairs that were housed together and all partners were kept consistent throughout the study (with one exception, see (Ostoji, Shaw, Cheke, & Clayton, 2013, p. 4127)). This means that the pairs would have already spent many feeding and gift giving sessions together (on their own, if not also in other experiments). So, if more time spent observing their female partners means that males will develop a 'better' ability to read the behavioural cues of their female partners, and the pairs have already spent an extended period of time together prior to the current study, then we would expect to see this 'better' ability in play during both the seen and unseen conditions. That is, even if the males from this study were excellent readers of their female partners' behavioural cues, we would not expect to see an increase in the males' gift-giving success rates between the seen and the unseen conditions. The fact that the males' success rate in choosing an appropriate gift was higher in the seen condition than in the unseen condition means that the increase in success in the seen condition is not likely due to the reading of behavioural cues.

A final experiment was done in order to test another alternative hypothesis. This hypothesis was that the male jays in the seen condition were simply developing specific satiety themselves by watching their female partners being pre-fed. In this experiment, males were allowed to watch their female partners being pre-fed on one of two food types: M or W. After having observed the pre-feeding, the females were taken away and the males were then presented

with two bowls of food: one of M and one of W. The amounts of the two food types eaten by the male jays after watching their females being pre-fed did not suggest that they had developed specific satiety, and so this alternative hypothesis was rejected.

These experiments on the food sharing habits of the Eurasian Jay done by Ostoji et al. provide important evidence for ToM in birds. Alternative explanations for the males' gift giving in accordance with females' desire states were found to be unlikely. The male's choice of gifts cannot be explained by the reading of behavioural cues, the representation of the male's own desire states in his female, or the development of specific satiety in the male from observing his female being pre-fed. Ostoji et al. concluded that the results provide evidence for self-other differentiation and the ability to represent the mental states of other birds in Eurasian Jays. That the male jays were able to successfully deliver the female's preferred food type is best explained by their ability to represent the desire states of their females. When a male jay watches his female partner being pre-fed, he mentally puts himself in the position of his female partner and using the input available to her, simulates her mental mechanism using his own. The male is then able to represent his female partner as having a particular mental state (in this case a desire state) and uses that representation to provide her with the most desirable food item.

2.3 Cooperation

Paal & Berezkei (2007) argue that there is an important connection between cooperation and the ability to represent the independent mental states and processes of others. They also note that this ability brings two important advantages for interacting socially, (Davies & Stone, 2003; Slaughter & Repacholi, 2003):

“First, it makes it easier to cooperate with others by facilitating the development of mutual attunement among the group members, which is a prime necessity for successful cooperation. Second, a well-developed ability to attribute mental states to others enhances competitive skills as it enables individuals to gain advantageous positions or, in certain cases, manipulate others in order to realize their own goals” (Paal & Berezkei, 2007, p. 542)

In this section I will examine evidence that birds can cooperate as well as evidence that birds are able to manipulate others in order to realize their own goals. I will argue that these behaviours are made possible by a bird’s ability to represent the mental states of its conspecifics.

2.3.1 Cooperation in Keas

Tebbich, Taborsky & Winkler (1996) performed a study in which they assessed whether Keas were able to cooperate in an instrumental task in order to retrieve a food reward. The Keas were tested in both dyad and group situations. In the instrumental task, at least two individuals needed to cooperate by manipulating an apparatus before they could obtain a food reward. The apparatus was designed so that one bird had to hold down a lever arm while the other bird retrieved the food reward from a newly uncovered box. Only one bird was able to retrieve the food reward.

The results of this study clearly showed that a bird’s place in the group’s social hierarchy determined the role that it played. Due to the nonlinear hierarchy of the group, the birds changed roles depending on the other birds they were cooperating with. In dyadic situations, the dominant bird always retrieved the food reward while the submissive bird always operated the lever arm. In group situations, the bird operating the lever arm was always submissive to at least one of the other birds in the group. Dominant Keas used manipulation to force their submissive partner into cooperation. When the submissive Kea tried to access the reward end of the

apparatus, the dominant Keas used aggressive approaches to force the submissive Kea back to the lever end of the apparatus. From that point in the first trial, and in all subsequent trials, the submissive Keas consistently held the lever role while the dominant Keas consistently held the reward role. These results show that it is unlikely that the birds were merely appearing to cooperate as they attempted to retrieve the reward individually since the birds continued to play distinct roles from trial to trial, depending on their rank in the group's social hierarchy.

Having a ToM is important for cooperation because without an understanding of a conspecific's mental states, birds would have to rely on accidental cooperation in order to solve problems like the one in this experiment. Similarly, this ability is what allows the dominant Kea to use social manipulation to force the submissive Kea to cooperate. The submissive Kea needs to be able to represent the dominant Kea's goal/desire state in order to make a decision of how to act cooperatively with the other Kea(s). Without this representation, submissive Keas may interpret their conspecific's aggression in any number of ways, but it would not be obvious that this aggression is meant to get the submissive Kea to pull down on the lever arm.

2.3.2 Cooperative Hunting in Brown-Necked Ravens

Yosef & Yosef (2010) observed Brown-Necked Ravens in the wild and reported that the Ravens worked cooperatively in teams of four to six to hunt Egyptian Mastigure lizards, a lizard that the Ravens could not hunt as individuals. The lizards live in burrows in the desert. Yosef & Yosef observed that the Ravens wait until the lizard is out of its burrow before they begin their attack. First, two Ravens go in and block the entrance to the burrow. Then the next two to four Ravens come in and attack the lizard. Only once the lizard is dead do the two Ravens blocking the entrance to the burrow leave their post to take part in the eating of the lizard.

This behaviour in the Ravens illustrates that the birds are aware of the role each member of the group is playing during the hunt. This is exhibited when the first two Ravens, blocking the entrance to the lizard's burrow, remain at the entrance to the burrow until the rest of the group has successfully killed the lizard. ToM allows each bird to represent the other group member's goals and intentions so that it may act accordingly in order to cooperatively hunt the lizard.

Though explaining this cooperative behaviour in terms of ToM is reasonable, it is important to note that this specific behaviour in Brown-Necked Ravens has only been documented in two locations within the same Valley and has not been studied in an experimental environment. This means that there may still be alternative explanations for the Ravens' behaviours. There have been other documented cases of cooperative hunting in Common Ravens (Hendricks & Schlang, 1998), though many of these reports are based on observations from the wild rather than from experimental settings. In order to best support the hypothesis that cooperation in birds is made possible by ToM, further experimentation is needed. Until then, there is still good reason to believe that ToM makes cooperative hunting in birds possible.

2.4 Some Birds Do Have a Theory of Mind

All of the behaviours studied in chapter two provide evidence for ToM in birds. Food caching behaviours in Western Scrub-Jays (and Ravens) can be explained by a bird's ability to represent the knowledge states and intentions of other birds. Cachers mentally put themselves in the position of the observing conspecific and use the input available to the observer to run their decision making mechanism in place of the target's mechanism. This type of simulation is process driven. With the representation of the observer as knowledgeable of cache location and

having the intention to pilfer the caches, the cacher is able to employ a number of different strategies in order to reduce the chances that its caches will be stolen. Some of these strategies attempt to degrade an observer's knowledge states by reducing the clarity of the visual information available to the observer or by confusing the observer.

Gift giving behaviours of the male Eurasian Jay are explained by the male's ability to represent the desire states of his female partner. The male jay, while observing his female partner being pre-fed to the point of specific satiety, mentally puts himself in the position of the female and uses the input available to the female (in this case pretend input as he is not actually eating the food items being pre-fed to the female) in order to run his decision making mechanism. Through this process driven simulation, the male is able to represent his female as having a particular desire state. Using this representation of his female's desire state, he is able to gift the appropriate food item to her.

Cooperative behaviours on instrumental tasks in Keas and in hunting in Brown-Necked Ravens are again explained by the representation of the mental states of conspecifics. During scenarios where they must cooperate in order to retrieve a food item, dominant Keas manipulate submissive Keas in order to force them into cooperation. This cooperation is made possible by a bird's ability to represent the intentions and goals of conspecifics. With the representation of the dominant Kea's goal, the submissive Kea is able to act in accordance with that goal. Similarly, cooperative hunting in Brown-Necked Ravens is made possible by the ability to represent the intentions and goals of their conspecifics. With the representations of the other birds' intentions and goals, a Raven within a hunting group is able to perform a unique role in order to make the hunt successful.

All of these behaviours can be explained in alternative ways that do not require a ToM. However, in the food caching studies alternative explanations were addressed thoroughly and found to be unlikely explanations for the birds' behaviours. Alternative explanations were also found to be unlikely through observations in Ravens. Though the documentation of these behaviours in Ravens is important, the fact that these observations were not made in experimental settings means we must be cautious of alternative explanations for the Ravens' behaviours. In the gift giving studies alternative explanations were again addressed in experimental settings and were again found to be unlikely. As the studies on the gift giving behaviours of the Eurasian Jays are still very new, I predict that in time we will see further variations on the studies discussed here which will produce results that confirm the hypothesis that the male jays are representing the desire states of their female partners. Studies done with Keas showed that cooperation is unlikely to be accidental and is better explained by ToM. Studies done with Ravens also confirmed their ability to cooperate. Although the finding that wild Ravens exhibit cooperative behaviours is important evidence for ToM in birds, the fact that these observations were not made in experimental settings with strict controls means that we must be cautious of alternative explanations in these cases.

In light of examining the empirical evidence on food caching behaviours, gift giving behaviours, and cooperative behaviours in birds, we have good reason for accepting the hypothesis that birds have the ability to represent conspecifics as having particular mental states that are different from their own. Alternative explanations were considered, explicitly in some cases, and found to be unlikely. The ability to represent conspecifics as having particular mental states that are different from one's own easily explains the food caching, gift giving, and cooperative behaviours exhibited by members of the Corvid and Parrot families. The hypothesis

that birds have a ToM offers the best explanation for these behaviours as it explains the most cases with the fewest assumptions. For this reason, we should accept that birds have a ToM.

Chapter 3: Objections and Replies

Now that I have examined the empirical evidence for ToM in birds and explained how this ability in birds is possible, I will consider and reply to some important objections to the argument that birds have a ToM.

3.1 Birds Just Can't Have a Theory of Mind

In his (1982) paper "Rational Animals" Donald Davidson argues that in order to have any form of thought or reason, a creature must be capable of having beliefs. Davidson says,

"First, I argue that in order to have a belief, it is necessary to have the concept of belief. Secondly, I argue that in order to have the concept of belief one must have language" (1982, p. 324)

From here, Davidson concludes that if non-human animals do not have language, then they do not have any form of thought or reason. By extension, we can conclude from Davidson's argument that since language is necessary for holding propositional attitudes (such as beliefs, desires, intentions, etc.) and non-human animals do not have language, that non-human animals are not capable of representing the mental states of conspecifics.

Though I agree that we have no reason for believing that birds have language, I disagree with Davidson in that I do not believe language is necessary for having a ToM. If birds do have beliefs, they are not represented in linguistic form in the avian brain. Though humans may have linguistic representations, birds do not. Elisabeth Camp (2009) has argued that some animal beliefs may be based on imagistic representational systems. Camp says that these imagistic systems can account for the social knowledge that baboons have and eliminate the need for a language of thought. A bird's representations are likely of this sort. They are based on

perceptual information and are dynamic. Though it is convenient for us to talk about a bird's representations in a linguistic way, for example "the cacher has the representation that 'the conspecific will steal my food,'" this does not mean that a bird's representations must be linguistic in nature.

3.2 Birds are Too Different

In a follow up paper to Premack & Woodruff's (1978) paper "Does the Chimpanzee Have a Theory of Mind?" Josep Call and Michael Tomasello (2008) review the empirical evidence for a ToM in chimpanzees. Call & Tomasello say that,

"All of the evidence reviewed here suggests that chimpanzees understand both the goals and intentions of others as well as the perception and knowledge of others. Moreover, they understand how these psychological states work together to produce intentional action; that is, they understand others in terms of a relatively coherent perception-goal psychology in which the other acts in a certain way because she perceives the world in a certain way and has certain goals of how she wants the world to be. There is much less evidence overall, but it is possible that other non-human primate species also have a similar understanding, and as do, perhaps, some bird species as well," (2008, p. 191).

From this, Call & Tomasello conclude that the answer to Premack & Woodruff's questions depends on one's definition of ToM. They say that if ToM is construed in a broad sense, then yes chimpanzees (and likely birds) do have a theory of mind. However, if ToM is construed in a more narrow sense, and animals are required to have the same kind of ToM that humans have, then chimpanzees (and likely birds) do not have a ToM since they are not able to understand that others have mental representations that determine their actions even when these mental representations are not consistent with reality. That is, if ToM is construed in non-human animals the same way that it is construed in humans, then non-human animals do not have a

ToM. I agree with Call & Tomasello's conclusion, but will argue further that ToM should not be construed as meaning the same thing in non-human animals as it does in humans.

To require non-human animals to have the same kind of ToM and be able to represent the same types of mental states that humans can in order for them to have a ToM is unreasonable. Even among humans there is a wide range in ToM sophistication. Some humans are able to represent certain mental states better than others, and some are unable to represent certain mental states at all. Requiring that non-human animals have the same sophisticated ToM that an adult human has would not only deny non-human animals a ToM, but it would likely deny some humans the ability as well. Birds are not able to represent the mental states of conspecifics at a level anywhere near to that at which humans do. Birds have a basic ToM but it is a ToM all the same.

3.3 The Studies are Wrong

In their (2007) paper "On the Lack of Evidence that Non-human Animals Possess Anything Remotely Resembling a 'theory of mind'," Derek Penn and Daniel Povinelli argue that there is no evidence for ToM in non-human animals. Though Penn & Povinelli focus primarily on studies done with chimpanzees, they also argue that the same problems arise in studies done with Corvids. Penn & Povinelli set out to answer four questions: what would it mean for a non-human and non-verbal animal to have a representation of a conspecific's mental state, what should and should not count as evidence for a non-human animal's understanding of a conspecific's mental states, why are current experiments failing to provide evidence for ToM in non-human animals, and what kind of experiments can provide evidence for ToM in non-human animals? Penn & Povinelli maintain that they are not concerned with how the ability to represent

conspecifics as having mental states that are different from one's own is made possible. That is, Penn & Povinelli remain agnostic as to whether ToM is best explained by TT, RT, ST, or an alternative explanation. For the purpose of their 2007 paper, Penn & Povinelli are simply concerned with whether or not non-human animals have the ability to represent the mental states of others, regardless of how this ability is made possible. Penn & Povinelli say:

“The only condition that must be met in order to qualify as a ToM, by our minimalists standards, is that the system must be able to produce and employ a particular class of information, namely information about the state of these cognitive variables from the perspective of that agent *as distinct from the perspective of the system itself*,” (2007, p. 733).

ToM is thus defined by Penn & Povinelli as “[the ability] to infer the state of the unobservable cognitive variables that will influence the behaviour of another agent using information observed from the perspective of the system itself,” (2007, p. 733).

Penn & Povinelli's main complaint about ToM studies in non-human animals is that they fail to create situations in which the information contained in the representations of a conspecific's mental states is not causally redundant with the information contained in the animal's own mental states, perceptual input, or feedback from the animal's sensorimotor loops “...including online and offline emulators,” (2007, p. 732). This choice in vocabulary is interesting. If by ‘feedback from the animal's sensorimotor loops including online and offline emulators’ Penn & Povinelli are referring to information produced through process driven simulation, then they have ruled out, by definition, a ToM that is made possible by process driven ST. However, since they claim to remain agnostic on the best explanation for ToM in birds, it seems odd that they would rule process driven ST out. Then I take Penn & Povinelli's main complaint about ToM studies in non-human animals to be that they fail to create situations

in which non-human animals must rely on representations of a conspecific's mental states that are different from their own mental states. Indeed, Penn & Povinelli argue:

“The available evidence suggests that chimpanzees, corvids and all other non-human animals only form representations and reason about observable features, relations and states of affairs from their own cognitive perspective. We know of no evidence that non-human animals are capable of representing or reasoning about unobservable features, relations, causes or states of affairs or of construing information from the cognitive perspective of another agent. Thus, positing [a ToM], even in the case of corvids, is simply unwarranted by the available evidence.” (2007, p. 737).

However, it is not clear to me that this is in fact the case. The (2006) study done by Dally, Emery & Clayton (discussed in section 2.1.4) provides evidence that birds are able to represent conspecifics as having mental states that are different from their own mental states. Indeed, not only were the birds able to represent conspecifics as having knowledge states that are different from their own, they were able to represent the different knowledge states of different conspecifics. The special role that the representations of the knowledge states as different from the cacher's own knowledge states play here is seen in the birds caching behaviour when multiple observers were introduced. In this experiment cachers were allowed to cache only in tray A in the presence of observer A, only in tray B in the presence of observer B, and a different cacher C was allowed to cache in tray C in the presence of observer D. When the original caching bird was allowed to recache in the presence of observer A, the cacher only recached items from tray A. When the cacher was allowed to recache items in the presence of observer B, the cacher only recached items from tray B. Finally, in the presence of observer D, the cacher did not recache items from either tray. If the cacher were simply representing the observers as having the same mental states as itself, then there would be no reason for this behaviour. By contrast, if the cacher were representing the different mental states of the observers as different from its own mental states, then the cacher should only recache items from the trays observed by

the observer present during the recovery phase. The results of this control condition showed that this is indeed what the cachers did. Cachers were able to successfully represent and keep track of the unique knowledge states of different observing conspecifics.

Similarly, Ostoji, Shaw, Cheke, & Clayton's (2013) study on the gift giving habits of male Eurasian Jays (discussed in section 2.2) also provides evidence that birds are able to represent conspecifics as having mental states that are different from their own mental states. In this study males were allowed to observe their female partners being preferred a particular type of food item to the point of specific satiety. The males were then able to gift the desired food item to their female partners. The alternative explanation that the males were simply representing their female partners as having their own desire states was explicitly tested for and found to be unlikely. This study also provides good evidence for a bird's ability to represent a conspecific as having a mental state that is different from its own mental state.

Both of these studies provide evidence of the type Penn & Povinelli claim is missing. These studies suggest that birds are able to represent the unique mental states of conspecifics. The contributions to the study of ToM in non-human animals made by Penn & Povinelli in their 2007 paper are extremely important for the field. Penn & Povinelli brought to attention a common failure of many studies and made clear the need for strict criteria for what should count as evidence of ToM in non-human animals and what should not. However, based on the results of Dally, Emery & Clayton (2006) and Ostoji, Shaw, Cheke, & Clayton (2013), Penn & Povinelli's claim that there exists no evidence for ToM in non-human animals is wrong.

3. 4 Conclusion

Premack & Woodruff's (1978) famous question launched the scientific study of ToM in non-human animals. Much of this research has focused on the great apes. In the past ten years or so, more and more studies on birds are appearing and this focus is beginning to shift. The gap that was once thought to exist between the great apes and all other animals is closing. Though humans still have by far the most sophisticated ToM, we no longer have good reason for believing that this ability is unique to humans.

I began my examination by clarifying what a ToM in non-human animals would be. I defined ToM as the ability to represent a conspecific as having a particular mental state that is different from one's own. I took this definition to be the same across all animals, despite possible differences in how mental states may be represented and in what kinds of mental states may be represented. I acknowledged that there is a wide range in the complexity that an animal's ToM can have and argued that birds remain at the bottom of this spectrum.

In the second chapter I examined the empirical evidence surrounding ToM studies in birds and presented an argument for ToM in birds. I considered the plausibility of this argument in light of alternative arguments and found that we have good reason to believe that birds have a ToM. Through the examination of empirical evidence and the ToM literature I have come to three conclusions. First, there is no reason to outright reject the possibility of a ToM in birds. Arguments that theoretically rule out the possibility that birds can represent the mental states of conspecifics are unreasonable. Though language may (or may not) play an important role in a human's ToM, language is not necessary for a ToM. Furthermore, recent findings on the DVR in avian brains provide evidence that birds have the necessary cognitive processing power

required for a ToM. My second conclusion, and my primary claim, is that we have good reason for accepting the hypothesis that birds do have a ToM. The food caching behaviours of Western Scrub-Jays, the gift giving habits of male Eurasian Jays, and the cooperative behaviours of Keas and Brown-Necked Ravens are all best explained by the ability to represent conspecifics as having mental states. Though alternative explanations for these behaviours exist, careful experimental design made these explanations unlikely, especially when considering all cases together. My third conclusion is that birds are able to represent the mental states of conspecifics through process driven simulation. Birds are able to represent the mental states of other birds by mentally putting themselves in the position of a conspecific and running their own mental mechanism with the input available to the target. This allows a bird to simulate the mental states of the target. By representing the mental states of conspecifics, a bird is able to predict the behaviour of its conspecifics and employ a number of evolutionary advantageous strategies.

Having the ability to represent conspecifics as having mental states is an impressive cognitive feat. For a long time, this ability was thought to be uniquely human. The idiom “birdbrain” is a clear example of the expectations humans had for avian cognition. We now have reason to reject this idiom. Members of the Corvid and Parrot families are extremely intelligent animals and they are capable of more complex cognition than we ever imagined. Birds interact within complex social systems and exhibit behaviours that were previously only observed in the great apes. We have good reason to believe that birds have a ToM.

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