4

How to Build a Scrub-Jay that Reads Minds

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1. Introduction

Although the search for human-like theory of mind (ToM) in non-human animals has continued unabated for almost 30 years, we have made very little progress in determining the psychological processes involved in non-human social cognition compared to the significant progress made in human infants. The underlying assumption that forms the basis for this research, is that ToM did not appear de novo in the evolutionary record of humans. Therefore, other animals, and most notably monkeys and apes, should at least demonstrate some of the precursors of socio-cognitive processing demonstrated by *Homo sapiens*. For example, there is good evidence that many animals follow another's line of sight to external objects (e.g. monkeys; apes; dolphins; domestic dogs; goats; seals; ravens; Grey parrots, see Emery 2000 for review). However, this ability need not be explained in mentalistic terms, as in many cases it may be purely reflexive (Povinelli and Eddy 1996). Indeed, this simpler explanation seems likely based on the generality of the behaviour, and the number of species in which it has been demonstrated.

The presence or absence of ToM in non-human animals becomes more controversial when we examine more sophisticated forms of social cognition, such as visual perspective-taking, knowledge attribution and false-belief (Emery 2005). Many chapters in this volume will attest to the sophisticated mind-reading skills of a wide variety of species, however, the plain and simple truth is that no non-human animal will ever demonstrate human ToM. As such, we should change our experimental focus onto what constitutes a species-specific social cognition. This is the aim of this chapter.

2. Why Comparative Social Cognition may be Failing?

We suggest that there are three reasons why comparative social cognition may be failing to achieve its goals. First, there appears to be little appreciation of the 3Es (ecology, ethology and evolution), both in the design of experiments and in

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thinking about what social cognition might be used for in the natural behaviour of an animal. By ecology, we mean environmental constraints on cognition, such as diet, habitat as well as social/mating system. Perhaps the best example is the case of food-caching corvids in which there are differences between species in performance on a variety of spatial memory tasks, which reflect differences in the ecology of the species (Balda et al. 1996). Clark's nutcrackers live at high altitudes in which food is scarce during the long, cold winter, they tend to eat and cache a very restricted diet (pine seeds), and they cache up to 30,000 pine seeds each year. By contrast, western scrub-jays live in a much more temperate climate at a much lower elevation, with a more varied diet, and which cache a lot fewer pine seeds (approx. 6,000 per year).

In laboratory tests for spatial memory, including cache retrieval, the Clark's nutcrackers tend to outperform the western scrub-jays, demonstrating greater accuracy for remembering cache location after long periods, or performing well on other spatial memory tasks not related to caching. However, Clark's nutcrackers and western scrub-jays not only differ on the amount of seeds cached and the habitat in which they live, but also in sociality. Clark's nutcrackers are territorial, and solitary (except during the breeding season), whereas western scrub-jays are semi-territorial and often form small flocks outside of the breeding season (Balda et al. 1996). Both Clark's nutcrackers and western scrub-jays are relatively asocial when compared to the closely-related pinyon jay, which routinely gather in flocks of 80 individuals, forming linear dominance hierarchies (Balda 2002).

Based on this ecological information, we would predict that in tests of sociality, pinyon jays should outperform both Clark's nutcrackers and western scrub-jays. Pinyon jays appear to use transitive inference to represent conspecifics' relative dominance status (Paz-y-Mino et al. 2004). Furthermore, they also seem to learn non-social versions of a transitive inference problem faster than western scrub-jays (Bond et al. 2003), however the scrub-jays eventually learn the task, and in the same way as the pinyon jays.

Furthermore, in a test of social cognition; observational spatial memory (which allows a cache pilferer to accurately locate another's caches); Clark's nutcrackers successfully locate another's caches even after a 1-day interval. They are less successful at a 2-day interval, compared to pinyon jays which are successful at this longer delay (Bednekoff and Balda 1996a,b). Western scrub-jays have only been tested at relatively short delays (3 hr), but are almost as accurate as the storers in locating their caches (Clayton et al. 2001). Data of this sort suggest that ecological information is necessary, but not sufficient for designing and interpreting biologically valid tests of comparative social cognition.

An appreciation of evolution is also important when considering species differences in cognitive ability. Let us return to the comparison between Clark's nutcrackers and pinyon jays. A phylogenetic reconstruction of the evolution of caching by corvids suggests that intense caching evolved independently in these two different lineages of corvids, and consequently there is no a priori reason to assume that the two species have developed the same solution to the problem of having to remember the location of so many food caches (de Kort and Clayton

2006). Consequently, the two species might have different problems when tested on tasks that rely on spatial memory, and closely related species might show more similar levels of performance than more distantly related ones.

To illustrate the point, we shall consider two comparative studies of spatial memory in corvids. In the first, Olson and colleagues compared pinyon jays and Clark's nutcrackers with the western scrub-jay and the Mexican jay, both of whom are moderate cachers, for their performance on an operant spatial delayed non-matching to sample (DNMTS) task using a touch screen (Olson et al. 1995), the pinyon jays were no better at this task than the other two jay species. The pinyon jay's performance was more similar to those of its close relatives, the scrub-jays and Mexican jays, despite being a specialised food-storer like the Clark's nutcracker.

In a second study, Gould-Beierle (2000) compared the performance of Clark's nutcrackers, pinyon jays, western scrub-jays and jackdaws on a radial maze. The Clark's nutcracker's performance was no better that that of the non-caching jackdaw, while both were outperformed by the pinyon jay and scrub-jay. As in the previous example, de Kort and Clayton (2006) point out that explanatory power comes from considerations of evolutionary relatedness: the nutcrackers are more closely related to jackdaws than they are to the two species of New world jay, despite the fact that Clark's nutcrackers are intense storers and known for their remarkable spatial performance in a variety of other spatial tasks.

The third E is ethology, and clearly understanding an animal's ethology or their natural behavioural repertoire is also important. In the case of social cognition, this means recognising examples of natural behaviour that may require mind-reading or in which social cognition provides an adaptive advantage over not having socio-cognitive abilities. Examples that have formed the basis for successful research programs are food competition in chimpanzees, caching and pilfering in corvids, and dog-human communication. We will focus our discussion to cache protection in corvids. Other potential examples, which have yet to be exploited by researchers, are cooperation in the formation of coalitions and alliances, and redirected aggression.

A second difficulty with comparative social cognition research has been the bias towards comparisons with humans, and consequently a focus on folk or naïve psychology (theory ToM) rather than alternative forms of social cognition, such as simulation ToM. This approach may have set up a "straw man" by which all non-linguistic creatures (non-humans and preverbal infants) will fail, as this approach is dependent on the development of language (Smith 1996). We will argue later in the chapter that the alternative simulation ToM approach may be better to test for social cognition in pre-verbal or non-verbal creatures.

Finally, until very recently comparative social cognition was not particularly comparative. Studies tended to be restricted to a small number of species, largely monkeys and apes. This has changed a little in the last few years, including work on domestic dogs (Hare and Tomasello 2005), foxes (Hare et al. 2005), domestic goats (Kaminski et al. 2005), dolphins (Tschudin 2006) and various species of birds (see below). However, if we are to learn what were the evolutionary precursors to the socio-cognitive skills of humans, whether social cognition takes different forms in different taxa, and how it develops with and across species, we need to expand the range of species being studied to closely related (comparative), and distantly related (phylogenetic) species, as well as individuals at different stages of development (ontogenetic; Tomonaga 2006).

The last 10 years has seen an increase in the use of the ecological approach in the design of animal cognition experiments (Balda et al. 1996). This is especially important for those studies on species distantly related to humans, as it is not clear whether such experiments are directly comparable in species with different perceptual worlds (Bitterman 1975). The ecological approach provides an opportunity for the animal under investigation to demonstrate the "best" of its abilities, rather than an anthropocentric bias inherent in studies designed for human and non-human primates. This approach, by increasing ecological validity, also matches the animal's behaviour in the wild more closely than any study in an information poor environment using arbitrary stimuli (Kamil and Maudlin 1988; Shettleworth 1998).

3. Avian Social Cognition

Although many birds form large, complex social groups, and form close relationships with other group members that resemble those found in some mammals, notably primates, elephants and cetaceans (Emery et al. 2007), the cognitive mechanisms by which birds may process social information (avian social cognition) has only recently become a viable topic for study. This is largely because of recent changes in our perception of birds as cognitive creatures.

The avian brain has, for over 100 years, been seen as a much simpler structure than the mammalian brain. The vast majority of the mammalian brain is cortical, neural tissue formed into six-layers of cells with both vertical and horizontal connections. The neocortex and particularly the prefrontal cortex, is involved in cognitive processing; thinking, memory, planning and social interaction. The neocortex was adapted from the pallium, whereas the equivalent area of the avian forebrain was traditionally seen as being adapted from the striatum (basal ganglia; Striedter 2005). The basal ganglia is involved in species-typical behaviour (sex, parenting, feeding, etc.) which is unlikely to be based on cognitive processing. Therefore the potential for intelligence in birds was seen as being constrained by their brains. However, recent data on the evolution, structure, neurochemical composition and function of the avian forebrain has demanded a re-evaluation of the cognitive skills of birds. Indeed, the majority of the avian forebrain has been renamed as pallial rather than striatal based on these studies (Avian Brain Nomenclature Consortium 2005; Emery and Clayton 2005; Reiner et al. 2004), suggesting that birds do have the brains to support the complex forms of cognition so-far only described for large-brained mammals.

Not all birds were created equal. Some families of birds, such as *Corvidae* (crows and jays) and *Psittacidae* (parrots) share many biological, ecological, neurobiological and behavioural traits with primates (Emery 2006); as such they may provide an example of convergent evolution (e.g. evolving analogous solutions to a similar problem), whereas others do not. We have suggested that the cognitive abilities of corvids and apes may also represent a case for convergent evolution, but with divergent evolution of neural systems (Emery and Clayton 2004a,b). As such, this provides us with a theoretical standpoint to investigate more complex forms of cognitive processing than would be possible if we had to base our investigations on out-dated models of comparative psychology that do not consider the 3Es and assume that all animals are intellectually equal (MacPhail 1987).

The study of social cognition in birds has had a relatively short history, largely because of the species of birds tested (pigeons, quail or chickens), the negative bias against complex cognition in birds because of their presumed small brain size and suggested limited flexibility in behaviour and because of a primatocentric bias. Although some of the best evidence for social learning comes from birds (Lefebvre and Bouchard 2003; Zentall 2004), the fact that birds are so distantly related to humans has made the design of suitable experiments a difficult stumbling block to progress. Also, contrary to the views of many, some species of birds demonstrate complex patterns of behaviour that are deployed flexibly depending on the context (e.g. innovation and tool use; Lefebvre et al. 1997, 2002).

Early studies found that birds perceived eyes and eye-like stimuli as aversive (Jones 1980; Scaife 1976a,b) supposedly representing the frontal orientation of a predator. Although chickens react strongly to the presence of two eyes and less so to one eye (maybe representing a predator looking away), frontal head orientation appears to be a sufficient cue to elicit strong aversive reactions in sparrows (Hampton 1994).

Studies on more complex aspects of social cognition, which have been tested on primates and other social mammals, did not occur until very recently (largely because of the reasons described above). For example, ravens can follow the gaze direction of a human experimenter behind a barrier (Bugnyar *et al.* 2004). Bee-eaters react to the visual perspective of a human "predator" approaching their nest from different directions, although this is likely based on computing the orientation of the human's face in relation to the nest rather than any understanding of what humans can or cannot see (Watve et al. 2002). African grey parrots appear to use a human's attention to learn about the names of objects (Pepperberg and McLaughlin 1996). In corvids at least, a sudden increase in interest in the socio-cognitive skills of birds can be attributed to a shift in using the caching paradigm to examine cache protection strategies as opposed to spatial memory. These experiments will form the basis for the rest of this chapter.

4. Cache Protection Strategies as Social Cognition

4.1. Biology of Cache Protection

Food-storing corvids, such as jays and ravens, cache food for future consumption and rely on memory to recover their caches at a later date. Food caching and recovery are activities which occur within a social context, not least because caches are susceptible to pilfering by other individuals, both other food-storers and also non-storing heterospecifics such as jackdaws (Dally et al. 2006b; Vander Wall 1990). For pilferers, the ability to locate caches made by others quickly and efficiently may be the important difference between successful pilfering and potential aggression from the storer. So an obvious advantage of observational learning of food cache location is that it allows birds to efficiently pilfer caches when others have left the scene, thereby eliminating both the costs of caching and of fighting (Clayton and Emery 2004). A number of corvids observe the caching behaviour of their fellow conspecifics, and show excellent spatial memory in locating another bird's food caches (e.g., Bednekoff and Balda 1996a,b; Bugnyar and Kotrschal 2002; Clayton et al. 2001; Heinrich and Pepper 1998).

The social context of caching behaviour may be viewed as a "cognitive arms race" between storers and pilferers, in which the storers use counter strategies to minimise the risk of having their caches pilfered (Bugnyar and Kotrschal 2002; Dally et al. 2006b; Emery et al. 2004). In this arms race, however, an individual bird can play both roles. Indeed, in highly colonial food-storers such as rooks, any member of a social group may play the role of both storer of its own caches and stealer of other individuals' caches depending on the circumstances. Field observations suggest that the storers engage in a number of cache protection strategies such as waiting until the would-be pilferers are distracted or cannot see them before they resume caching, or by making "false" caches that either contain a inedible item such as a stone or nothing at all (e.g. rooks, Kallander 1978; ravens, Heinrich 1999; Heinrich and Pepper 1998; Bugnyar and Kotrschal 2002). And, some corvids return alone to caches they had hidden in the presence of conspecifics, and readily re-cache them in new places unbeknown to the potential thief (e.g. jays, Emery and Clayton 2001, ravens, Heinrich 1999).

While field observations are of enormous value in documenting the natural behaviour of these birds, an experimental approach is crucial for understanding the mechanisms underlying these behaviours and determining the effects of experience, particularly in relation to "theory of mind" (Clayton et al. 2007). Consider the observation of birds moving the food they had hidden in the presence of other individuals, and re-caching the food items in new places when those observers were no longer present. In the wild, one might explain the presence or absence of another bird as purely coincidental to the caching and re-caching events. To test whether it is the presence of an observer at caching, and absence of one at recovery, that elicts the food-cacher's re-caching behaviour, Emery and Clayton (2001) allowed hand-raised western scrub-jays to cache either in private or while a conspecific was watching and then recover their caches in private. Individuals subquently re-cached food in new cache sites, but only when they had been observed during caching (Fig. 1). We argue that because the two conditions were identical at the time of recovery (in private), the birds had to remember whether or not they had been watched during the caching condition in order to know when to re-cache during recovery, and whether to re-cache in new sites. By focussing on the counter strategies of the storer when previously observed by

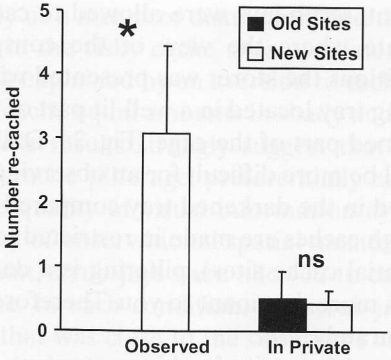

Fig. 1. Number of food items re-cached by storers during recovery in private; either when they had been observed during caching or had cached in private. Items were re-cached into either old sites (in the same tray) or new sites (different tray not made previously available). (Adapted from Emery and Clayton 2001, *$p < 0.05$)

a potential thief, this experiment raises the intriguing possibility that this re-caching behaviour is based on mental attribution.

Bugnyar and Kotrschal (2002) have also suggested that the storing and stealing tactics used by some food-caching corvids may involve complex social cognition. These authors suggest that ravens engage in tactical deception through an attempt to manipulate another's attention, either to prevent opponents from gaining opportunities to steal, or to gain opportunities for learning socially from their opponents. Raven cachers try to increase the distance between themselves and potential thieves, and often halted caching or re-cached based on the behaviour of the observers; whereas raiders also increased their distance from cachers. Bugnyar and Kotrschal (2002) argued that raven cachers appear to appreciate the visual perspective of potential raiders because they cache behind large objects (e.g. tree stumps and rocks) and position themselves in relation to the object and the observer so preventing the observer from ⟨seeing⟩ them cache. It is not clear, however whether the storers appreciate the concept ⟨see⟩ in others or whether they are merely responding to the fact that they cannot ⟨see⟩ the observer. This will be discussed further in the next section.

4.2. *Visual Perspective Taking*

A bird which caches in front of a conspecific may need to appreciate that individual's visual perspective to determine whether the potential thief will be able to use observational spatial memory to locate those caches at a later time. It would be inefficient to utilise protection behaviours with respect to caches which are not in danger, such as those that have not been seen. At the time of caching, a storer may assess the amount of visual information available to a pilferer and may either reduce that information *during* caching or move caches during recovery which have been *seen* during caching. We have investigated such cache protection strategies in three studies.

In the first experiment, scrub-jays were allowed to cache either in front of a conspecific or in private where the view of the conspecific was completely occluded. In both conditions the storer was presented with a choice of where to cache; either in a caching tray located in a well-lit part of the cage or in a caching tray located in a darkened part of the cage (Fig. 2a; Dally et al. 2004). The suggestion being that it will be more difficult for an observing scrub-jay to see where caches have been placed in the darkened tray compared to caches placed in the well-lit tray. Even though caches are made in restricted localisations (i.e. caching trays with only 8 potential cache sites), pilfering is a dangerous business, especially when the storer is more dominant to you. Therefore, pilferers need to steal caches quickly and accurately.

Although the scrub-jays' favourite food is wax worms, we provided them with pine nuts in this experiment, so that degradation of the worms under the heat of the sun lamp used to provide light to one side of the cage could not explain their behaviour. When the jays cached in private they cached equal amounts in both well-lit and darkened trays (Fig. 2b). By comparison, when the jays cached in front of a conspecific, they cached significantly more pine nuts in the darkened sites (Fig. 2b). In the observed condition, caching in the well-lit sites was suppressed compared to the darkened sites whereas it was not in the in private condition. These findings suggest that the birds were actively avoiding caching in the well-lit sites when observed, but not when they cached in private.

At recovery, the jays retrieved very few items from the trays, however of those caches that were recovered; the vast majority were removed from the well-lit tray and re-cached in new sites (Fig. 2c). One suggestion is that this function as an additional cache protection strategy; cache some items in "risky" cache sites, such

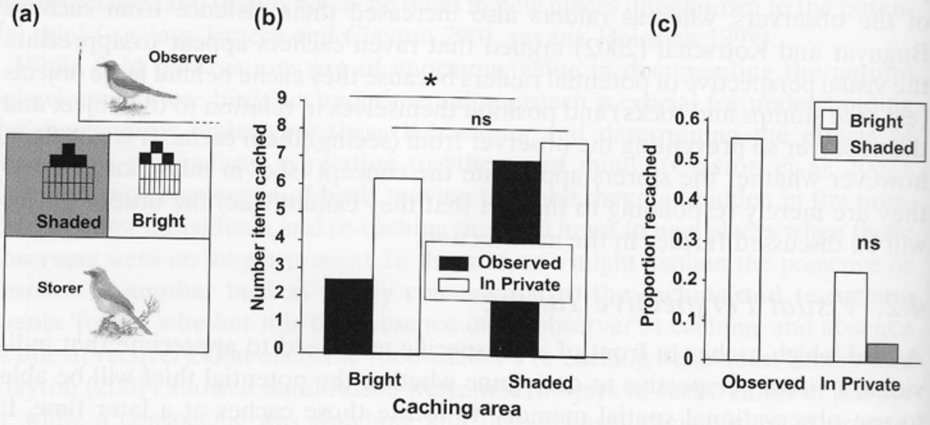

FIG. 2. Sun-shade experiment. **a** Schematic representation of experimental design. A unique caching tray is located in the shaded area of the cage and the bright area of the cage. **b** Number of food items cached in either bright or shaded trays; either when caching in private or when observed. **c** Proportion of food items re-cached from either bright or shaded sites; either when cached in private or when observed. (Adapted from Dally et al. 2004. *$p < 0.05$, ns $p > 0.05$)

as well-lit areas, possibly as a means of distraction, and then recover and re-hide those remaining items in the risky cache sites at a later time in private. These results cannot be readily explained by an aversion to cache in the light compared to the dark as the birds cache equal amounts in shady and well-lit areas in private (Dally et al. 2004). These results strongly suggest that western scrub-jays are sensitive to the risk of cache pilferage, preferentially caching in sites that will potentially degrade the quality of visual information available to pilferers and thus reduce the accuracy of observational spatial memory.

In a second experiment, scrub-jays were allowed to cache either in front of a conspecific or in private. In each condition, the scrub-jays were provided with two caching trays; one that was close to the observer's cage ("near tray") and a second that was relatively further away from the conspecific (i.e. at the back of the storer's cage "far tray"; Dally et al. 2005a; Fig. 3a). The suggestion being that it will be more difficult for a potential pilferer to steal caches made in sites further away either because they will focus their attention on those caches made closer to them or because the quality of visual information becomes degraded the further away a stimulus is located. When the scrub-jays cached in private, they cached equal amounts of wax worms in both the "near" and "far" trays. By comparison, when the storers cached in front of a conspecific they cached significantly more wax worms in the "far" tray than the "near" tray (Fig. 3b).

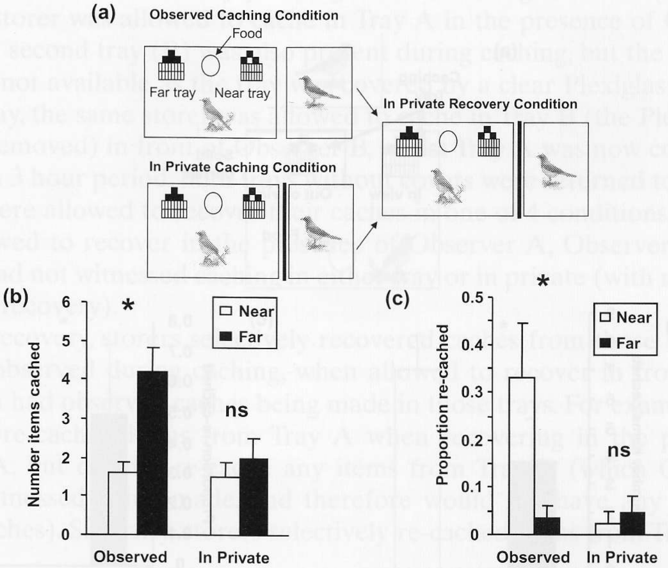

FIG. 3. Near-far experiment. **a** Schematic representation of experimental design. A unique caching tray is located close to a conspecific (near) and relatively further away (far). **b** Number of food items cached in either the near or far tray when cached in private or when observed. **c** Proportion of food items re-cached from either the near or far tray when the storer had cached previously in front of a conspecific (observed) or in private. (Adapted from Dally et al. 2005a, $^*p < 0.05$, ns $p > 0.05$)

At recovery, the majority of items that were re-cached in new sites were from the "near" tray and only when they had been cached in front of another scrub-jay (Fig. 3c). Similarly to those caches made in the well-lit tray in the previous experiment (Dally et al. 2004), the caches made in the "near" tray would have been the most at risk of any pilfering attempts, as they were the closest to the potential pilferer, with the clearest view of exactly where they had been made. As with the Dally and colleagues (2004) experiment, the suggestion for why scrub-jays do not put all there caches in the most protected tray (e.g. "far" tray) is that caching a few items in the "near" tray may function as a form of distraction. As observers did not get the opportunity to steal any caches in this study, the storers were given the opportunity to retrieve these high risk caches. We will return to the issue of why the storers use cache protection strategies at all in the laboratory setting later.

In the final experiment investigating visual perspective taking, scrub-jays were provided again with two caching trays, but always with another bird present. In this study, one half of the storer's cage was occluded by a solid metal sheet. One caching tray was located behind the barrier which prevented the conspecific from observing any behaviour directed towards caches made in this "out of view" tray. A second tray was located in the other half of the storer's cage, but in full view of the conspecific, therefore the observer could see any behaviour directed towards caches made in this "in view" tray (Fig. 4a; Dally et al. 2005a). In this study, birds

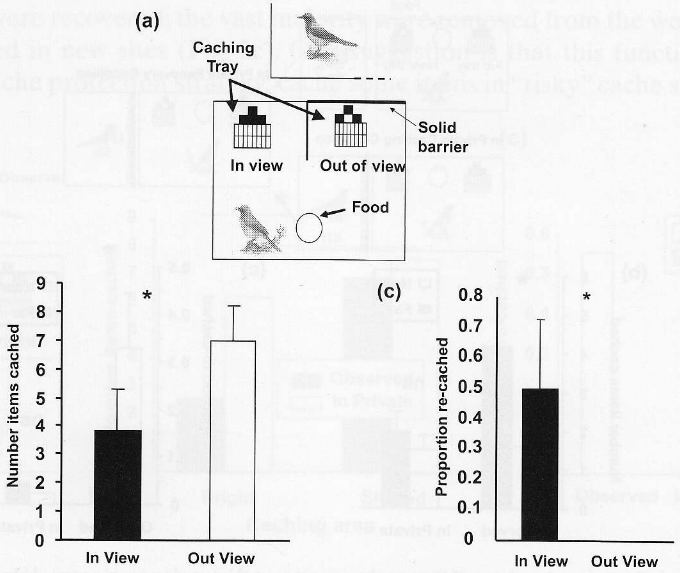

FIG. 4. Barrier experiment. **a** Schematic representation of experimental design. A unique caching tray is located "in view" and "out of view" (behind barrier) of a conspecific. **b** Number of food items cached; either in view or out of view. **c** Proportion of food items re-cached from either in view sites or out of view sites. (Adapted from Dally et al. 2005a, $*p < 0.05$, ns $p > 0.05$)

that either appreciate that another bird cannot see them if they cache behind a barrier, or prefer to cache out of sight of a conspecific, should choose to cache in the "out of sight" tray rather than the "in view" tray. Indeed, during caching, the storers preferentially hide caches in the "out of view" tray, however as before, they do place about 25% of their caches in the riskier "in view" tray (Fig. 4b).

At recovery, we found a similar pattern of results to the previous studies, in which the storers tended to re-cache items from the risky sites in the "in view" tray rather than the "out of view" tray (Fig. 4c). Therefore, in all three studies, the scrub-jays cached a few items in sites which the observers could see them clearly (well-lit, in the open or close) and the majority in the more protected sites. In every case, the storers returned to the riskier cache sites and re-cached those items in new places that the observer would have had no knowledge.

4.3. Knowledge Attribution[1]

The studies by Emery and Clayton (2001) and Dally et al. (2004, 2005a) suggest that storing scrub-jays may appreciate the different knowledge states of observers; if they had ⟨seen⟩ specific caches being made in tray A, they should be ⟨knowledgeable⟩ about the caches in A, whereas, if they did not ⟨see⟩ caches being made in tray B then they should be ⟨ignorant⟩ about the caches in B.

We therefore tested scrub-jays using a similar design to this (Dally et al. 2006a). A storer was allowed to cache in Tray A in the presence of Observer A (Fig. 5a). A second tray (B) was also present during caching, but the cache locations were not available as the tray was covered by a clear Plexiglas strip. After a short delay, the same storer was allowed to cache in Tray B (the Plexiglas strip had been removed) in front of Observer B, whilst Tray A was now covered (Fig. 5a). After a 3 hour period, both trays without covers were returned to the storer, and they were allowed to recover their caches in one of 4 conditions. They were either allowed to recover in the presence of Observer A, Observer B, a naïve bird who had not witnessed caching in either tray or in private (with no bird able to observe recovery).

During recovery, storers selectively recovered caches from those trays which had been observed during caching, when allowed to recover in front of those birds which had observed caches being made in those trays. For example, storers selectively re-cached items from Tray A when recovering in the presence of Observer A, but did not re-cache any items from Tray B (which Observer A had not witnessed being made, and therefore would not have any knowledge of these caches). Similarly, storers selectively re-cached items from Tray B when

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[1] It should be noted that knowledge attribution has also been investigated in magpies (Prior and Güntürkün, unpublished observations) and ravens (Bugnyar and Heirich 2005), but we do not have the space to go into the details of these experiments. Although the results from both studies are extremely interesting, they do not possess the same levels of control as the scrub-jay experiments (Dally et al. 2006a), and consequently the results can be explained in terms of behaviour-reading, rather than mind-reading.

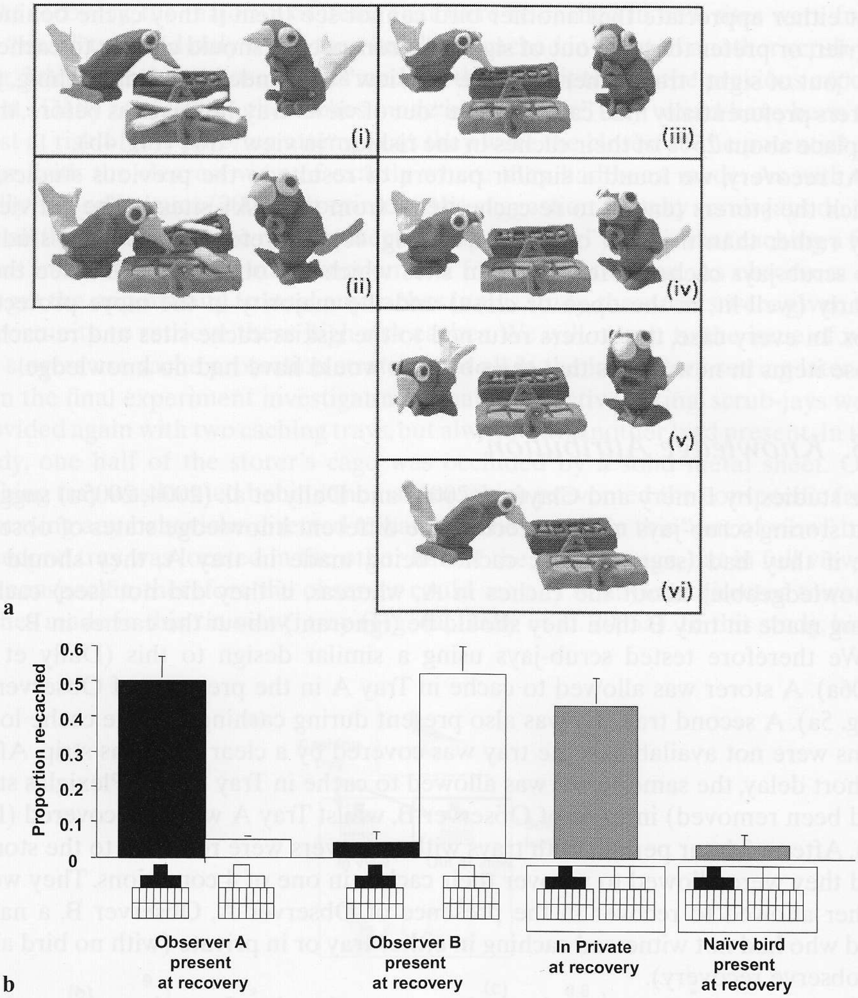

FIG. 5. Knowledge attribution experiment. **a** Schematic representation of experimental design. **i.** Storer caches in Tray A in front of Observer A, Tray B is covered with clear plastic; **ii.** Storer caches in Tray B in front of Observer B, Tray A is covered with clear plastic; **iii.** Storer recovers from Trays A and B in front of Observer A; **iv.** Storer recovers from Trays A and B in front of Observer B; **v.** Storer recovers from Trays A and B in front of a naïve conspecific (C) and **vi.** Storer recovers from Trays A and B in private. **b** Proportion of food items re-cached, either when in the presence of Observer A, Observer B, a naïve bird or in private. **c** Number of food items re-cached at recovery; **i.** re-cached from both trays into old and new sites during in private condition, **ii.** number of times food items moved in the in private condition, **iii.** re-cached from both trays into old and new sites during observed condition and **iv.** number of times food items moved in the observed condition. (Adapted from Dally et al. 2006a)

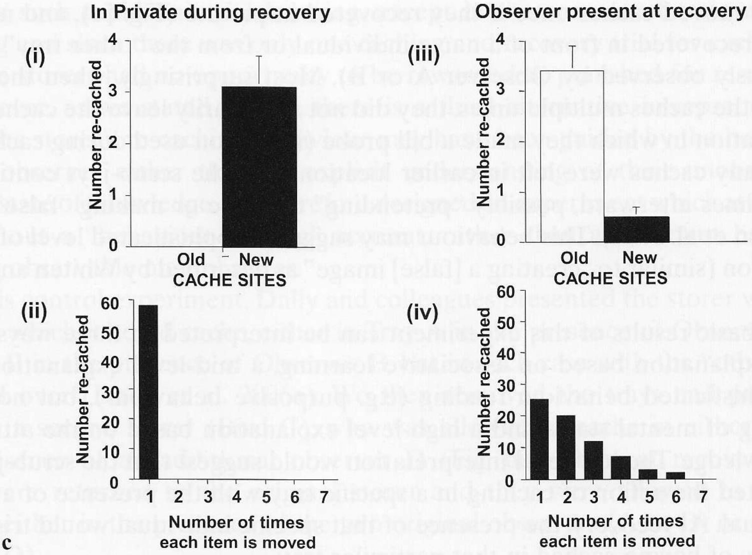

FIG. 5. *Continued.*

recovering in the presence of Observer B, but not from Tray A which Observer B had not witnessed being cached in (Fig. 5b).

By contrast, storers did not re-cache items from either tray when recovering in the presence of the naïve bird, suggesting that they attributed "ignorance" to that bird, which had not seen caches being made in either tray. Re-caching in front of the naïve bird would have provided them with information they previously did not have. Finally, the storers re-cached items from both trays when they recovered in private, as Observers A and B had seen caches being made in these trays, and so re-caching them in private would move the caches to new places which potential pilferers had not seen. This condition replicates earlier studies of re-caching in private when previously cached observed (Emery and Clayton 2001; Emery et al. 2004).

At first glance, re-caching in front of another bird does not seem like the most sensible strategy to protect caches. Indeed, dominant birds may not need to re-cache at all, and may defend their caches aggressively (Dally et al. 2005b). However, birds of a lower status should move their caches if they had been observed because of the threat provided by a pilferer with observational spatial memory. But, moving caches in front of another bird should provide new information on any new cache site. We therefore viewed the videotapes of recovery behaviour in detail, and noticed that the storers did not just move their caches only one time; they moved them up to 5–6 times during the short recovery period, but they only moved those caches which had been made in "observed trays" (i.e. Tray A in the presence of Observer A and Tray B in the presence of Observer B; Fig. 5c).

They moved caches once if they recovered in private (Fig. 5c), and not at all if they recovered in front of a naïve individual or from the "other tray" (i.e. not previously observed by Observer A or B). Most surprisingly, when the storers moved the caches multiple times, they did not necessarily leave the caches in the last location in which they made a bill probe (i.e. action used during caching). In fact, many caches were left in earlier locations, but the scrub-jays continued to a few times afterward, possibly "pretending" to cache or making "false" caches (Clayton et al. 2007). This behaviour may suggest a sophisticated level of tactical deception (similar to "creating a [false] image" as described by Whiten and Byrne 1988).

The basic results of this experiment can be interpreted in three ways; a low-level explanation based on associative learning, a mid-level explanation based on sophisticated behaviour-reading (e.g. purposive behaviour), but no understanding of mental states and a high-level explanation based on the attribution of knowledge. The low-level interpretation would suggest that the scrub-jays had associated the action of caching in a specific tray with the presence of a specific individual. At recovery, the presence of that specific individual would trigger the memory of having cached in that particular tray.

The mid-level explanation would suggest that the storers were in-tune with behavioural cues produced by the observers, such as spending more time attending to the tray they had cached in. As such, the storer was doing nothing more than reacting to the behaviour of the observer at the time of recovery. By contrast, the high-level interpretation would suggest that the storers not only remembered which particular individual was present during specific caching but also attributed different mental states to these individuals based on their presence ("knowledge") or absence ("ignorance"). The knowledge attribution would also need to be definitive to particular individuals in specific contexts, given that both observers were both knowledgeable of some caching events and ignorant of others. For example, Observer A had "knowledge" of the location of caches in Tray A, but was "ignorant" of caches in Tray B, and vice versa. The high-level interpretation may be reasonably convincing for corvids and apes, which have passed the higher level stages of object permanence (Bugnyar et al. 2007; Pollok et al. 2000; Tomasello and Call 1997).

However, what credence do these lower level interpretations have? Heyes (1998), for example, explained the results of earlier experiments on knowledge attribution in chimpanzees by Povinelli et al. (1990), as a form of associative learning; an individual was either present or absent during baiting and therefore simple associations could form based on presence ("knowledge") and absence ("ignorance"). This simpler explanation could also explain the selective re-caching behaviour of the scrub-jays, albeit it is more sophisticated as it has to be based on integrating information from the past (social context during caching) with planning for the future (potential pilfering by the observer). Note that the jays' behaviour cannot be explained in terms of differential familiarity with the two trays because both trays were always present during caching, although only one of them was available to cache in. Finally, no current associative theory explains such rapid one-trial learning, except in the context of taste aversion learning and since there was only one caching and recovery trial for each condition, the storers had no opportunity to be rewarded or punished for re-caching.

However, as we stated earlier, there is a third alternative interpretation, in which the storer's re-caching behaviour may have been guided by the behaviour of the observer rather than an explicit understanding of their unobservable mental state of knowledge. We therefore designed an experiment which attempted to rule out a "behaviour-reading" account, rather than an account based on reading observable mental states.

In this control experiment, Dally and colleagues presented the storer with two trays in which it could cache, either in Tray A in the presence of Observer A or in Tray B in the presence of Observer B, but in each case with the "other tray" covered over (Dally et al. 2006a). We then removed the trays and presented then to a second storer (Bird C), who was allowed to cache in either tray in the presence of an additional observer D (Fig. 6a). Then, at recovery, both trays were returned to the original storer and they were allowed to recover caches, either in the presence of the two original observers (A or B) or the new storer (D).

If the storer based their re-caching decisions on the behaviour of the observer bird, independent of whether or not they were present during caching in a particular tray, then the storer should have re-cached items equally from both the "observed tray" and the "other tray" because Observer D had witnessed caching in both trays (although by a different storer, C). Observer D should therefore have attended both trays equally, and so both trays would be equally at risk. By contrast, if the storer was attributing knowledge to the observer, they should, as shown previously, only re-cache items from the "observed tray". Indeed, the

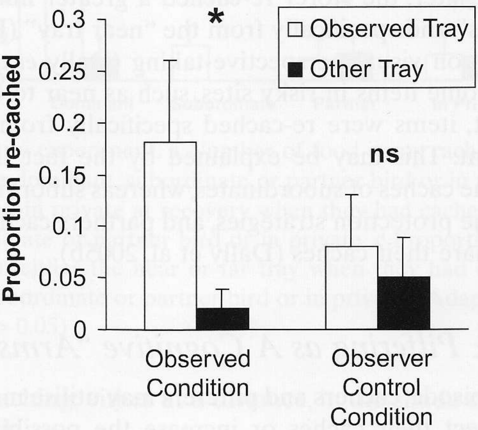

FIG. 6. Proportion of food items re-cached from either the observed tray or the other tray in the Observer condition or from either the observed tray or the other tray in the Behaviour-reading control condition. (Adapted from Dally et al. 2006a)

re-caching behaviour described earlier was repeated in the same observer condition (selectively re-cache from the "observed tray") whereas for the new behaviour-control condition (with Observer D), very little re-caching occurred, and what did was not significantly different between the two trays (Fig. 6b). We therefore suggest that it is unlikely that the storer was using behavioural cues from Observer D to influence their re-caching decisions.

4.4. Does It Matter Who's Watching?

One potential problem with the previous control experiment is the fact that the new observer (D) was completely new to the storer. There is abundant information which suggests that many birds, including corvids, can recognise individuals either by voice or by visual appearance. Therefore, it is likely that the storer recognised this particular individual, and remembered that they were not present at the time of caching, and therefore treated them similarly to the naïve bird in the original experiment (Dally et al. 2006a), and so not re-cache. Also, the observer might respond differently depending on whether the bird was the same as the one present at caching.

There are additional clues that scrub-jays recognise which individual was watching during caching based on the protective actions they utilise during cache recovery. Storers were allowed to cache in either a near tray or a far tray, either in front of a dominant conspecific, a subordinate conspecific, their partner or in private. The storers cached significantly more items in the far tray when caching in front of a conspecific, independent on which class of individual; dominant, subordinate or partner (Fig. 7a; Dally et al. 2006a). There were more caches made in front of the dominant individual than in front of the subordinate or partner.

At recovery 3 hr later, the storer re-cached a greater number of items from the "dominant trays" and specifically from the "near tray" (Fig. 7b). As with the earlier experiments on visual perspective-taking (Dally *et al.* 2004, 2005a), the scrub-jays cached some items in risky sites, such as near to the observer. In the current experiment, items were re-cached specifically from the "near tray" in front of a dominant. This may be explained by the fact that dominant birds aggressively steal the caches of subordinates, whereas subordinates have to resort to more subtle cache protection strategies, and partners cache readily in front of one another and share their caches (Dally et al. 2005b).

4.5. Caching & Pilfering as A Cognitive "Arms Race"

During a caching episode, cachers and pilferers may utilise many different strategies to either protect their caches or increase the possibility to steal caches without the subsequent threat of aggression from the storer. As yet, we do not know what strategies pilferers use to increase the chances with which they will successfully steal another's caches, but we suggest that they will be similar to those used by storers. For example, we suggest that it will aid a thief to hide

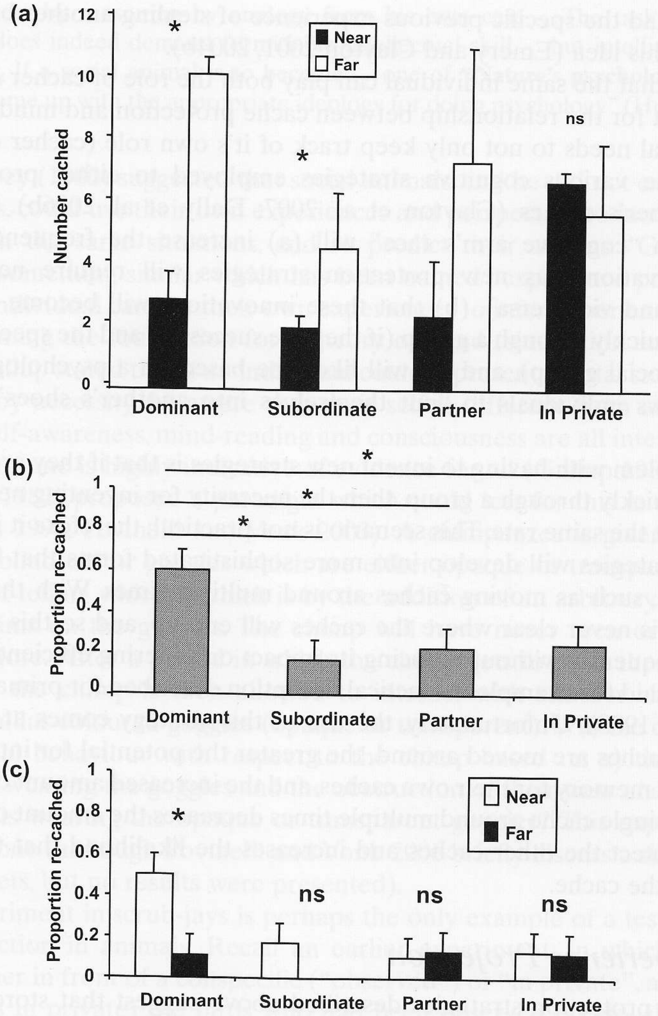

FIG. 7. Observer identity experiment. **a** Number of food items cached in either the near or far tray in front of a dominant, subordinate or partner bird or in private. **b** Proportion of food items re-cached in private at recovery when they had cached previously in front of a dominant, subordinate or partner bird or in private. **c** Proportion of food items re-cached in private from either the near or far tray when they had cached previously in front of a dominant, subordinate or partner bird or in private. (Adapted from Dally et al. 2006a. $^*p < 0.05$, ns $p > 0.05$)

themselves during caching; either at a distance, in the shade or behind a barrier, such as a tree or rock.

It is not clear how such strategies and counter strategies may have evolved, however, the use of such strategies in a flexible manner, as described for the previous experiments, suggests complex cognition and a high degree of innovation. Indeed, the fact that cache protection strategies are not employed until a storer has had the specific previous experience of stealing another bird's caches reinforces this idea (Emery and Clayton 2001, 2004b).

The fact that the same individual can play both the role of cacher *and* pilferer is important for the relationship between cache protection and mind-reading, as an individual needs to not only keep track of it's own role (cacher or pilferer), but also the various cognitive strategies employed to either protect caches or steal other's caches (Clayton et al. 2007; Dally et al. 2006b). We suggest that such a "cognitive arm's race" will (a) increase the frequency of novel social innovations (as new protection strategies will require new pilfering strategies, and vice versa), (b) that these innovations will become transmitted relatively quickly through a group (if they are successful and the species involved lives in a social group), and (c) will likely be based on a psychological system which allows individuals to "put themselves into another's shoes" (discussed below).

The problem with having to invent new strategies is that if they are successful, and pass quickly through a group, then the necessity for inventing new strategies increases at the same rate. This scenario is not practical; therefore it is likely that existing strategies will develop into more sophisticated forms that become less predictable, such as moving caches around multiple times. With this particular strategy, it is never clear where the caches will end up, and so this strategy can be used frequently without reducing its impact on pilfering efficiency. The same cannot be said for examples of tactical deception described for primates (Whiten and Byrne 1988). Unfortunately, the use of this strategy comes at a price; the more the caches are moved around, the greater the potential for interference of the storer's memory for their own caches, and the increased amount of time taken to move a single cache around multiple times decreases the amount of time available to protect the other caches and increases the likelihood that the observer might see the cache.

4.6. Experience Projection

The cache protection strategies described above suggest that storers have not only equipped themselves with a vast array of different cognitive tools to counter the potential for pilfering, but also that these abilities may require the storer to place themselves "inside the head" of a pilferer and use the specific counter measures to counter what they would do as a pilferer in the same situation. This in itself suggests sophisticated abilities hitherto not described for other non-human animals. These abilities imply something which has been termed *experience projection*. Humphrey (1980) was perhaps the first to suggest that inward reflection or introspection was an essential part of understanding other social beings.

> "a revolutionary advance in the evolution of mind occurred when, for certain social animals, a new set of heuristic principles was devised to cope with the pressing need to model . . . the behaviour of other kindred animals. The trick which Nature came up with was introspection . . . it proved possible for an individual to develop a model of the behav-

> iour of others by reasoning by analogy from his own case . . . The task of modelling behaviour does indeed demand formidable intellectual skill . . . but intelligence alone is not enough. If a social animal is to become . . . one of **"Nature's psychologists"** it must somehow come up with the appropriate ideology for doing psychology" (Humphrey 1980, p. 59).

Humphrey (1980) suggested that social animals, and he did not explicitly state which ones, could use their own experiences and perspective to model another's thoughts in the same situations, and so predict their actions.[2] Gallup (1982) suggested something similar which has been named "experience projection", in which an individual can use their own experiences to infer experiences in others, and so forming the foundation for a theory of mind (simulation and empathy). Indeed, Gallup stated that if an individual could represent mental states in others it should, by necessity, be aware that their self is different from another's self. As such, self-awareness, mind-reading and consciousness are all inter-linked, and evidence for one is highly indicative of evidence for all (Gallup 1982).

Gallup (1982) proposed a paradigm which could test for this in animals (see also Heyes 1998; Povinelli and Vonk 2003). A chimpanzee is given experience wearing a blindfold or goggles which are either opaque or transparent, but the only way of telling which is which is by the addition of an arbitrary cue, such as coloured rims on the goggles. The chimp will have never seen or worn these goggles before. After a period in which the chimp gets to wear these two types of goggles, the chimp is then allowed to interact with another chimp who is wearing similar coloured goggles (opaque or transparent). Will the chimp adjust their normal behaviour with respect to the chimp based on a) their previous experience wearing the goggles and the obstruction of their view and b) whether the chimp is wearing the opaque or transparent goggles? This experiment has yet to be done (although Povinelli and Vonk 2006 briefly discuss a similar design using buckets, but no results were presented).

An experiment in scrub-jays is perhaps the only example of a test for experience projection in animals. Recall an earlier experiment, in which scrub-jays cached either in front of a conspecific ("observed") or "in private", and at recovery (always in private) the birds who had been observed previously re-cached food items primarily into new sites, whereas when they had cached in private they performed very little re-caching and did not differentiate between old and new sites (Emery and Clayton 2001). Before this study, the birds were tested for observational spatial memory and split into three groups (Clayton et al. 2001). One group were allowed to cache wax worms in trays (Storer group) and later recover them in private, a second group watched the storer cache and were then allowed to find their caches and steal them (Observer group) and a third group were located in an adjacent cage to the caching bird, but the view between them was occluded, so they could only hear them caching (Control group). The birds

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[2] Clayton et al. (2007) argue that the western scrub-jay falls into Humphrey's category of being one of "Nature"s psychologists.'

in the Observer group were almost as accurate in locating caches as the birds in the Storer group, whereas the Control group birds were poor at finding caches (Clayton et al. 2001).

Importantly for the Emery and Clayton (2001) study, these three groups had different experiences based on caching and pilfering. The Storer group (Clayton et al. 2001) had experience of caching and recovery, and had seen other birds caching, but had never been given the opportunity to pilfer another jay's caches. Consequently, this group was renamed the Observer group in the Emery and Clayton (2001) study. The Observer group in the Clayton et al. (2001) study had experience of observing other's cache, and had been given the opportunity to steal those caches, and so was re-named the Observer + Pilfer group (Emery and Clayton 2001). Finally, the Control group in the Clayton et al. (2001) study had experience of pilfering other birds caches, even though they had not seen them being made, and so were re-named the Pilfer group (Emery and Clayton 2001). We do not suggest that the Pilfer group had never seen another bird caching, only that in these particular studies they had not been given any specific experiences of observing and pilfering the *same* caches.

We were interested in whether these different experiences would lead to differences in the presence or absence in the use of cache protection strategies. Indeed, the Observer + Pilfer, and the Pilfer groups demonstrated an identical pattern of results; re-caching a large proportion of items from the tray in which they had previously been observed caching, and moving them to new sites (Fig. 8a,b). By contrast, the Observer group without any experience of being a

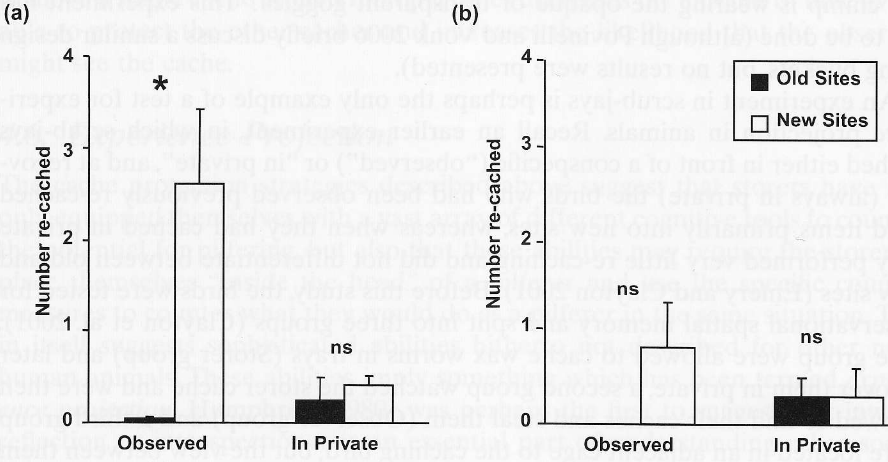

FIG. 8. **a** Number of food items re-cached by Pilfer group into old or new sites when they had been previously observed during caching or had cached in private. **b** Number of food items re-cached by Observer group into old or new sites when they had previously been observed during caching or had cached in private. (Adapted from Emery and Clayton 2001)

pilferer themselves re-cached very few, if any items (Emery and Clayton 2001; Fig. 8c). Therefore, we suggest that storers with the specific experience of stealing another's caches (even when they had not seen the caches being made), *project* this experience onto another bird, namely one which is observing their caching, and so is a potential thief.

Therefore, during recovery the storers with pilfering experience have to (a) remember the previous social context during caching (i.e. whether they were observed or in private), (b) reflect on their previous pilfering experience (i.e. what they did when observing and pilfering), and (c) use this experience to guide their decisions about what to do with their caches when no observer is present (i.e. re-cache in new sites which the observer has no recourse to search in).

It is not clear how this pilfering experience may be represented in the scrub-jay brain (however a proposal will be discussed in the final section). This issue is particularly intriguing with respect to the Pilfer group. In the observational memory study (Clayton et al. 2001), these birds did not see another bird caching and thus only pilfered caches they had not seen being made. How did these birds ⟨know⟩ that they were pilfering another's caches and not recovering their own without some understanding of self versus other? The birds did have experience of hearing another bird cache, although it would have been difficult to differentiate the sounds of caching from recovery. They also may have a natural tendency to search opportunistically for caches. However, these two factors do not explain how the birds could differentiate between caches they had made and caches others had made.

One might suggest that all these birds had to do was remember that they did not cache in these particular trays (as each tray was unique). Although these birds did not have experience of stealing caches made by other birds, they had considerable experience of caching and recovery from similar looking trays, so it likely that they had generalised that all trays which resemble trays in which they had previously cached in, also contain caches. However, to translate the action of removing caches not made by them into the specific experience of being a pilferer, and the subsequent action of re-caching in new sites when they had previously caching in front of a conspecific, suggests more than this simple explanation. It is hard to reconcile without some form of understanding about own versus other.

We can be fairly certain that it was the act of being a pilferer rather than being pilfered from which was the relevant experience, as all birds in these groups will have been pilfered from, as they had all taken part in studies of episodic-like memory (e.g. Clayton and Dickinson 1998) in which all caches were removed by the experimenters before recovery to test for memory. Only the Observer + Pilfer group and the Pilfer group had had pilfering experience.

4.7. *But Is It "Theory of Mind"?*

A sceptic might be quick to say that what the scrub-jays are doing is either sophisticated behaviour-reading in the case of cache protection strategies (as the observer is present during caching), or they are behaving based on a series of species-specific predispositions which enable them to become "in tune" with a pilferer's actions because this is biologically important (i.e. is a domain-specific form of cognition).

Although no one has yet to criticise the scrub-jay (or raven) social cognition studies in print, we would like to attempt to do so ourselves along the same lines as Povinelli (2000, Povinelli and Vonk 2003, 2006) and Heyes (1998) have done for chimpanzee social cognition studies, particularly those based on visual perspective-taking. We believe that this exercise will be useful in terms of collating evidence for theory of mind in scrub-jays, helping in the design of future experiments which might be less ambiguous in their interpretation, but also revealing whether alternative explanations are not sufficient to explain the scrub-jays' behaviour.

Povinelli's main criticism of the Leipzig group studies (e.g. Hare *et al.* 2000, 2001) is that the chimpanzees' behaviour (moving toward the hidden food) can be explained by a psychological system which represents another's behaviour (S_b) and by a system which represents another's behaviour plus their mental states (S_{b+ms}). Povinelli rightly suggests that folk psychology is constructed from an understanding of behaviour; therefore it is difficult to distinguish between the low-level S_b explanation and the high-level S_{b+ms} explanation (Povinelli and Vonk 2006). This argument is particularly cogent for the studies of visual perspective-taking, as the chimps can both see one another, and even when they cannot see one another at the start of the test, the subordinate will have seen the facial orientation of the dominant chimp, probably looking at the piece of food that both of them can. ⟨see⟩ The subordinate may therefore have avoided the piece they both could see and approached the other piece because the dominant was oriented towards the piece in the open, not because the subordinate knew that this was the piece of food that the dominant could ⟨see⟩.

Using Povinelli's methods, the mental states which might be involved in the Hare et al. (2000) study may be explained as follows:

(a) The subordinate chimp observes both pieces of food, one located next to a barrier, one located in the open;
(b) The dominant chimp observes one piece of food located in the open;
(c) The subordinate chimp concludes that because the food next to the barrier is hidden from the dominant's view, they cannot ⟨see⟩ it, whereas the food in the open can be ⟨seen⟩ by both chimps;
(d) The subordinate chimp approaches the food next to the barrier (because if the dominant could ⟨see⟩ the hidden food it would move towards and compete for it).

Section (c) tries to explain the subordinate's behaviour based on reasoning about mental states (⟨seeing⟩), however Povinelli suggests that removing this explanation does not affect the behavioural outcome of the experiment (i.e. that the subordinate still approaches the hidden food).

(a) The subordinate chimp observes both pieces of food, one located next to a barrier, one located in the open;
(b) The dominant chimp observes one piece of food located in the open;
(c) The subordinate chimp approaches the food next to the barrier (because chimps only approach food that is available to them).

In this case, an explanation that is not based on representing mental states is easy to reconcile, as chimps will have had many previous occasions (outside of the experiments) in which a dominant will get access to food when presented, but will not get food that is not within their field of view. This analysis falls down, however, when learning and experience cannot account for the behaviour (see later). What of the scrub-jays? Using the same methodology, we will describe the various visual perspective-taking experiments, and determine whether S_b has the same explanatory power as S_{b+ms}.

Let us consider the barrier experiment (Dally et al. 2005a), in which the scrub-jay either cached behind a barrier or in the open. Povinelli's description may go as follows:

(a) The storer is in the presence of an observer when the tray is in the open;
(b) The storer is alone when the tray is located behind a barrier;
(c) The storer concludes that because the tray is hidden behind a barrier, the observer cannot ⟨see⟩ the contents of the tray;
(d) The storer caches in the tray behind the barrier (because the observer cannot pilfer caches that it cannot ⟨see⟩).

In this example, the explanation based on reasoning about mental states (S_{b+ms}) does not do any additional causal work than the explanation based on reasoning about behaviour (S_b). The observer is either absent (when the storer caches behind the barrier) or present (when the storer caches in the open), therefore the decision of where to cache may be dictated by two conditional rules; "out-of-sight, out-of-mind", and "others are unlikely to steal caches if they were absent when the caches were hidden or caches are less at risk if they are hidden in private, behind barriers, in dark places, etc.":

(a) The storer is in the presence of an observer when the tray is in the open;
(b) The storer is alone when the tray is located behind a barrier;
(c) The storer caches in the tray behind the barrier as another bird is not present (and others do not steal caches when they were absent during caching).

In the wild, corvids tend to cache next to objects, such as rocks, tree stumps and changes in patches of grass (Bennett 1993; Bugnyar and Kotrschal 2002; Dally et al. 2006b; Helme et al. 2004, unpublished observations), however it is not clear whether this is because they act as landmarks allowing the caches to be easily found again by the storer, or as a form of protection against conspecifics seeing where the caches have been made (de Kort et al. 2006). In the Dally et al. (2005a) study, only one trial was provided for each condition, and consequently they had little opportunity to learn that caching alone results in little or no pilfering, whereas caching in front of others results in caches being stolen, particularly since these hand-raised birds had not had any prior experience with barriers. Nonetheless, the possibility remains that such rules are innate, or rapidly generalised from the previous social context of caching experiments (Clayton et al. 2001; Emery and Clayton 2001).

A more difficult case to explain by reasoning about behaviour alone is the sun/shade experiment (Dally et al. 2004). In that experiment, a storer was provided with 2 caching trays, one located in the dark and the other in the light. A Povinellian analysis would go along the following lines:

(a) The storer is in the presence of an observer with two caching trays; one in bright light, one in the dark;
(b) The tray in the light is easier to ⟨see⟩ than the tray in the dark, and so easier to pilfer from;
(c) The storer caches in the dark tray (because the observer cannot ⟨see⟩ the caches as clearly as those made in the bright tray).

However, if we remove the mental state reasoning from (b), then we are left with the following:

(a) The storer is in the presence of an observer with two caching trays; one in bright light, one in the dark;
(b) The tray in the light is more visible;
(c) The storer caches in the dark tray (because observers do not pilfer as successfully from dark trays).

A simple "out of sight, out of mind" discrimination of the type described for the barrier experiment does not work in this case, as the storer cached in both trays in the presence of another bird, and it was the trays which were different not the observers. Indeed, the only difference between the two trays (besides being visuo-spatially unique) was the amount of light projected upon them. One possibility is that the storers use a conditional rule based on an assessment of cache risk in which the observer's behaviour differed depending on whether the storer was caching in the well-lit tray or the dark tray.

It is not clear how this difference was manifest. Aside from an innate conditional rule, it is possible to conjure up a behaviour-reading account. For example, it is possible that the observer looked more closely at the caches made in the dark tray because it would be more difficult to see where the caches had been made (i.e. our functional explanation for why the storer cached more items in the dark tray). If the observer looked more closely, then we predict that the storer should have avoided caching in this tray, not increasing the amount, as was found. Of course, the opposite may have occurred where the observer could not have seen the caches being made in the dark tray and so lost interest and focused their attention onto the light tray, and consequently the storer avoided caching in the light tray. The storer did make most of their caches in the dark tray; however it seems unlikely that the observer would avoid looking at the tray in which the majority of the caches were made, if they were to use observational spatial memory to pilfer them at a later time.

Behavioural explanations of this experiment should also appreciate that the storer needs to use a second conditional rule, namely one about their own position with respect to the two trays and the observer, as both trays are present in both conditions ("observed" and "in private"), and it is the differential environment of the storer (in the dark or in the light) which predicts their behaviour.

The one problem with the behaviour-reading account is that it requires a series of very flexible conditional rules which can be applied to different individuals across a variety of different but particular contexts. For example, "Public Enemy Number One" is one of the more dominant scrub-jays in our colony who always looks out for pilfering opportunities, often using aggression to steal caches. As an observer, "Public Enemy Number One" looks intently at the caches being made and does not attempt to hide his "looking behaviour". By contrast, "Jack the Lad" is a subordinate scrub-jay who will pilfer when given the opportunity, but only when allowed to pilfer in private when the cacher has left the scene. As such, "Jack the Lad" has developed good observational spatial memory.

When "Jack the Lad" is cast as an observer, he tends to turn away from the cacher, or hide, particularly if the cacher is dominant, so as to avoid giving away his "pilfering intentions". Therefore, two different birds, two different pilfering strategies, and two different forms of behaviour which need to be read and interpreted based on identity and context. Furthermore, when "Sweetie Pie" caches then "Jack the Lad" is dominant, rather than subordinate, so he may look at the caches being made and revert to an aggressive strategy.

The behaviour-reading account also does not allow one to accurately predict the future behaviour of an unknown conspecific, as behaviour-reading is based on computing statistical regularities over the course of a relationship between two individuals. As western scrub-jays are semi-territorial, and cache protection may be primarily implemented to protect against theft by territory neighbours, it seems unlikely that such an unspecific method would be productive in preventing pilfering. In this case, understanding something about mental states, or being sensitive to complex conditional rules of the form described above, would appear to be the most biologically parsimonious explanation for their behaviour.

How does a Povinellian analysis stand up to the other experiments designed to test for epistemic states, such as ⟨knowledge⟩? To recap, in the Dally et al. (2006a) study, storers were presented with two trays (A & B) only one of which they could cache in (because the other was blocked access), in the presence of a specific observer (A or B). Therefore, they could cache in Tray A in the presence of Observer A, and cache in Tray B in the presence of Observer B. At recovery, both trays were available and storers could recover in the presence of Observer A or B, a naïve bird who had not been present at the time of caching or recover when alone. A Povinellian analysis may proceed as follows:

(a) The storer caches in Tray A in the presence of Observer A and access to Tray B is blocked;

(b) The storer then caches in Tray B in the presence of Observer B and access to Tray A is blocked;
(c) The storer concludes that only individuals who had ⟨seen⟩ caches being made will have ⟨knowledge⟩ of them;
(d) At recovery, the storer re-caches selectively from Tray A when in the presence of Observer A, and from Tray B when in the presence of Observer B because the observers have ⟨seen⟩ caches being made in these trays and so ⟨know⟩ their location. The storers do not re-cache from the other tray in the presence of the observers because they have not ⟨seen⟩ caches being made in those trays, and so will be ⟨ignorant⟩ of their location. The storers do not re-cache from either tray in the presence of an unknown observer as they have not ⟨seen⟩ any caching and so will be ⟨ignorant⟩ of all caches.

Again, removing the explanation based on reasoning about mental states (c) leads to the following revised explanation based solely on reading behaviour:

(a) The storer caches in Tray A in the presence of Observer A and access to Tray B is blocked;
(b) The storer then caches in Tray B in the presence of Observer B and access to Tray A is blocked;
(c) At recovery, the storer re-caches selectively from Tray A when in the presence of Observer A, and from Tray B when in the presence of Observer B because the observers directed behaviour [e.g. looking] towards the tray that was cached in when they were present or the presence of the observer triggered a memory of where they cached in the presence of the specific observer. The storers do not re-cache from either tray in the presence of an unknown observer as they were absent during caching, and pilfering does not occur in the absence of an observer during caching.

Although this low-level account may explain the action of re-caching (however, see below), it fails to explain the fact that the storers move caches around multiple times during recovery, and particularly when the caches are not placed in the final location in which the storer inserted their bill. We have already provided a functional explanation for this behaviour, which is that it aids to confuse the observer as to the new location of the caches; however it is not clear that a S_b is sufficient to explain the mechanisms involved. Perhaps, the storer waits to deposit the cache in a site when the observer is not looking or is distracted, and this influences the final cache site? This suggests a level of behaviour-reading so far not reported for any non-human animal. However, as unlikely as this scenario may be, the fact that it is possible presents a problem for our interpretation of this behaviour.

One argument against this suggestion is the result of our control experiment (Dally et al. 2006a). At recovery, the storer re-cached items from the "observed tray" when in the presence of a previous observer, but not from the "other tray", thereby replicating our previous experiment. In the observer control condition, in which a new observer is present when new caches are made by a new storer, the original storer does not re-cache many items, and does not differentiate between the two trays when in the presence of the new observer. We suggested that the storer rightly did not re-cache many items as they would have "recognised" that the new observer had not been present at caching. However, if the new observer looked more intently at one of the trays (i.e. the one they had witnessed caching in), then this should have been perceived by the storer. The storers did not appear to perceive such differences between the two trays, as there was no difference in the number of items re-cached from either tray. It remains to be determined which psychological process or processes are involved in this suite of protective behaviours.

For the final study to be considered (Emery and Clayton 2001), one might suggest that re-caching, even when performed in private, is elicited by a memory of the previous behaviour of the observing bird. This is difficult to reconcile with the results of an interleaved trials experiment in which the storers first cached in Tray A when observed, and then a short time later in Tray B when in private or vice versa (Emery and Clayton 2001). In this case, the storers displayed the same pattern of results at recovery as in the basic design; re-caching specifically from the tray in which they had cached when observed, and primarily in new sites. It is therefore hard to explain re-caching based on a general memory for the previous event or at a simpler level, a hormonal or other physiological stress response produced by being watched during caching. Indeed, if a simpler mechanism elicited re-caching it might predict generalised re-caching, not re-caching specifically in new places.

What level of explanation would be suffice for the fact that re-caching behaviour is not an automatic response, but is dependent on the storer having had previous experience of being a thief in the past? Let us try to reverse engineer the possible psychological mechanisms which may be involved at recovery to elicit re-caching.

First, the storer has to remember the previous social context of a previous caching event in relation to each tray (either bird present or absent). Second, the storer needs to use this social information to influence its current behaviour (re-caching) in anticipation of a future event (pilfering) independent of the present context (no observer present). Third, only jays with experience of being a pilferer transfer this experience to another bird, and so produce appropriate counter strategies (re-caching in new sites). Fourth, the idea that birds project their experience onto another bird may suggest a form of introspection. It is difficult to envisage how this could occur without recourse to some appreciation of the distinction between self and others.

5. Cognitive Architecture of the Scrub-jay Social Mind

The preceding analysis of the scrub-jays' behaviour in each of our experiments infers that their cache protection strategies are (a) rational (i.e. caused by the interaction of a belief and desire in such a way that performance of the behaviour in question fulfils the desire if the belief is true (and fails to do so if the belief is false; Clayton et al. 2006), (b) follows a logical progression, (c) based on a sophisticated understanding of the subtle behaviour of others which allow storers to predict the future actions of conspecifics, (d) based on the specific experience of being a pilferer and (e) maybe based on introspection.

If we conclude that western scrub-jays' cache protection strategies are rational, and therefore cognitive, we can use this information to construct a cognitive architecture of how scrub-jays do their psychology when competing with potential thieves (Fig. 9). We therefore present a cognitive architecture of the scrub-jay social mind inspired by a cognitive architecture of human mind-reading (Nichols and Stich 2003).

During recovery, a number of processing stages need to occur before a cache may be protected from pilferage. Information enters the PERCEPTION system to allow an assessment of the current social context; either the storer is alone or in the presence of other individuals. If the storer is in the presence of conspecifics, then their behaviour will also be assessed (e.g. eyes open or closed, direction of attention, direction of movement, vocalizations, emotional state, etc.). This information feeds into the BELIEF system, which alerts the bird to the possibility of theft; "*caches will be stolen by an observer who saw then being made*". The BELIEF system interacts with the DESIRE system which functions to motivate their response; "*protect caches from theft*". Information feeds into the DESIRE system from the INTERNAL ENVIRONMENT (e.g. motivational state). Information from the BELIEF and DESIRE systems passes to the DECISION

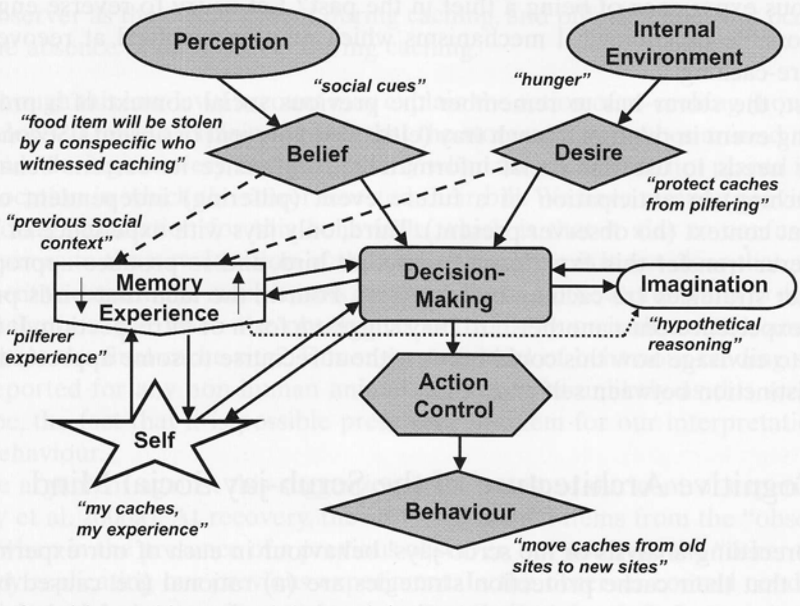

FIG. 9. Cognitive architecture of the scrub-jay social mind.

MAKING system, where the ultimate course of action (e.g. appropriate cache protection strategy) will be initiated. The DECISION MAKING system interacts with a number of different systems in order to make the correct decision. Alternative courses of actions may be rehearsed in the IMAGINATION system, allowing a storer to predict which actions will be expected to succeed, and which ones will fail. This system interacts with the MEMORY/EXPERIENCE system to provide information on which actions have been successful in the past. The MEMORY/EXPERIENCE system interacts with the BELIEF system as only thieves recognise the threat posed by conspecifics for cache safety. The MEMORY/EXPERIENCE system also provides information on the previous social context (either alone or in the presence of others). The MEMORY/EXPERIENCE system may also interact with a SELF system to determine that the experiences are "owned" by the storer and are not "possessed" by others. Once this information has been assimilated, and an appropriate course of action "decided" upon, the DECISION MAKING system communicates this decision to the ACTION CONTROL system, which initiates the appropriate behaviour (e.g. re-caching in new sites, moving caches around multiple times, hiding food in the shade, etc.).

6. Conclusions

We suggest that our detailed analysis of the different cache protection strategies used by western scrub-jays, and especially whether they require an understanding of behaviour alone or behaviour plus mental states, is good evidence for theory of mind in scrub-jays. We are particularly confident that we have provided good evidence based on Heyes' (1994) proposal for triangulation of evidence, and the important role of experience projection which is difficult to explain using behaviour-reading and simple associative theories of learning. Currently, studies on other non-human animals may be explained by behaviour-reading rather than understanding unobservable mental states. Of course, we do not propose that scrub-jays are particularly intelligent compared with other non-human animals, or that other animals do not have a theory of mind, only that the cache protection paradigm (and implementation of the 3Es) has provided us with an extremely useful tool with which to investigate these issues in non-verbal creatures based on their natural history. This ability to increase the ecological validity of experiments, although dismissed as unimportant by some (e.g. Povinelli and Vonk 2004), is an incredibly powerful weapon in our quest to learn more about the minds of other animals.

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