Cache protection strategies by western scrub-jays, *Aphelocoma californica*: implications for social cognition

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Food-caching western scrub-jays cache items themselves, and use observational spatial memory to steal the caches of others. Our aim in this study was to investigate the strategies used by scrub-jays to reduce cache theft by conspecifics. In three experiments, scrub-jays were allowed to cache wax worms in two different locations. In experiment 1, the birds preferred to hide items in distant sites when watched by another jay, but used near and distant sites equally when the observer's view was obscured by a screen. As conspecifics rely on observational spatial memory to steal other jays' caches, this use of distance might reduce the visual information available to the potential thief and thus decrease pilfering accuracy. Where possible, however, placing caches out of sight may be more effective. In experiment 2, storers cached predominantly in distant, out-of-view, sites. However, items placed in view of the observer were moved multiple times, possibly confusing the observer as to their location. In experiment 3, when in-view and out-of-view sites were equidistant to the observer, storers cached mainly in out-of-view sites when observed, but cached equally in both sites when not observed. During recovery sessions, when the storer was not observed, these items were selectively recached in new sites unbeknown to the observer. It may be advantageous not to hide all the caches in one place, because unpredictability might provide the best insurance against pilfering.

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The food-caching paradigm provides a naturalistic model for testing social cognition in several avian and mammal species. In many food-caching species, social context (the presence or absence of conspecifics) is important because caches are susceptible to theft by others (Brockmann & Barnard 1979; Heinrich & Pepper 1998; Emery & Clayton 2001). The risk of cache theft is particularly high in corvids, where conspecifics rely on observational spatial memory to pilfer, with a high level of accuracy, caches they have observed others make (Bednekoff & Balda 1996a, b; Clayton et al. 2001; Bugnyar & Kotrschal 2002). Andersson & Krebs (1978) argued that food caching could become an evolutionarily stable strategy only if the storing individual had a significantly higher probability of recovering its own caches than a conspecific had. This view has recently been the subject of debate. Both Smulders (1998) and Vander Wall & Jenkins (2003) have shown that it is possible for food caching to stabilize in a population independently of whether or not storers experience a high level of cache theft. However, the criteria on which

their models are based do not apply to food caching in corvids. For example, Smulders's (1998) model requires each individual in the population to have a separate foraging niche, but this foraging strategy is specific to parids (e.g. willow tits, *Parus montanus*: Brodin 1994; crested tits, *Parus cristatus*: Lens et al. 1994). The model developed by Vander Wall & Jenkins (2003) is based on solitary individuals (rodents), but western scrub-jays are semiterritorial (Curry et al. 2002). For all these reasons, western scrub-jays might be expected to experience a high level of cache theft and also to use cache protection strategies to minimize the chance of cache loss. To do so, storers should be sensitive to the risk that observers pose to their cache sites, and to use this information when implementing strategies to reduce cache loss.

Field observations suggest that storers engage in a number of cache protection strategies, such as waiting until would-be pilferers are distracted or cannot see before caching (e.g. common raven, *Corvus corax*: Heinrich & Pepper 1998; Heinrich 1999), or by caching in areas of low conspecific density (e.g. rook, *Corvus frugilegus*: Källander 1978; common magpie, *Pica pica*: Clarkson et al. 1986; common raven: Bugnyar & Kotrschal 2002). Some corvid species are also known to return alone to caches

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hidden in the presence of conspecifics, and recache them in new places unbeknown to potential thieves (e.g. western scrub-jay: Emery & Clayton 2001; common raven: Heinrich 1999; Eurasian jay, *Garrulus glandarius*: Goodwin 1955).

While field observations are of great value in documenting natural behaviour, an experimental approach is crucial for understanding the mechanisms underlying these behaviours and determining the effects of experience. To test whether it is the presence of an observer at caching, and the absence of one at recovery, that elicits the food-cacher's recovery behaviour, Emery & Clayton (2001) allowed hand-reared western scrub-jays to cache either when observed by a conspecific, or while alone, and then recover their caches when alone. Individuals with experience of pilfering another bird's caches subsequently recached food in new sites, but only when observed during caching. Because the recovery conditions were identical, the birds had to remember whether or not they had been watched during caching in order to know whether they needed to recache food items, and if so whether to cache into new sites. Only birds that had been thieves hid their caches in new places; naïve birds did not do so. This finding suggests that these individuals related information about their experience as a pilferer to the possibility of future theft by another bird, and changed their caching strategy accordingly. This may be a demonstration of high-level social understanding called experience projection (Emery & Clayton 2004).

Recaching items upon recovery is a cache protection strategy that is not without significant risk. In the field, pilfering is an immediate and constant threat, as observers have unrestricted access to the caching arena. Several species of corvid have been observed either to gather up food items and fly elsewhere upon the arrival of a conspecific (e.g. rook: Simmons 1970), or to drive observers away from the site of cached items, before subsequently recaching them (e.g. Eurasian jay: Wilmore 1977; Bossema 1979; Goodwin 1986; rook: Goodwin 1986). Yet, if observers are constantly present, a bird that refrains from caching in their presence, or that waits for them to become inattentive, forfeits the ability to exploit ephemeral food resources. Our aim in this series of experiments was to investigate whether scrub-jays implement cache protection strategies not only during recovery, but also at the time of caching.

EXPERIMENT 1: EFFECT OF DISTANCE

A recent experiment revealed that scrub-jays prefer to cache in shady sites in the presence of observers (Dally et al. 2004). A possible consequence of this strategy is that the visual information available to potential thieves becomes impoverished. This might be particularly effective because conspecifics rely on observational spatial memory when stealing other jays' caches (Clayton et al. 2001). Distance could also be used to reduce the transfer of visual information to the observer, and thus decrease the subsequent risk of cache theft from those observers. Alternatively, storers might always cache in sites furthest from other birds, regardless of whether the potential pilferers are observing the caching event, because the further away the cache site, the longer it will take the potential pilferer to reach it.

In this experiment, the storer had access to two caching sites, one of which was near to and one far from the observer, and the jays were given the opportunity to cache under two conditions, Private and Observed. If the jays are capable of implementing a caching strategy based on relative distance they should cache preferentially in distant sites. If distance is used specifically for reducing the transfer of visual information to observers, then this preference for maximizing distance should occur only when another jay can observe the caching event. Thus, when caching is private, storers should cache equally in both sites, provided that they do not use a default mechanism such as maximizing distance regardless of social context.

Methods

Subjects and apparatus

We used birds collected as nestlings in California, U.S.A. This was conducted under a Federal Fish and Wildlife permit and a State of California Collecting permit. The birds were subsequently hand reared and housed as a captive population at the University of California, Davis, before being imported via air transport to the U.K. (with a U.S.A. Fish and Wildlife export permit and MAFF import permit). They are currently housed at the University of Cambridge in accordance with the University of California and the University of Cambridge guidelines, and will remain so until the end of their natural life span.

We tested eight sexually mature birds ($N = 3$ females, 5 males). These birds had previously participated in an experiment in which they acted as both observers and pilferers. In this experiment, observers were given the opportunity to steal caches they had observed a bird in an adjacent cage make. We therefore predicted that these birds would treat observers as a threat to cache safety, even though they were housed in separate cages, and that they would use cache protection strategies to reduce the chance of cache theft. The jays were housed in individual cages (91×76 cm and 91 cm high) and were maintained inside at 20–22°C on a 12:12 h light:dark cycle and a diet of mixed nuts, dog biscuits, various fruits, wax worms, *Galleria mellonella*, and mealworms, *Tenebrio molitor*. The maintenance diet was removed from the home cage before an experimental trial (at 1800 hours) ensuring that the jays were mildly hungry during caching (at 1000 hours). Water was available ad libitum.

During caching, wax worms were presented in 15-cm-diameter bowls. Birds were able to cache in ice cube trays (6 cm wide $\times$ 25 cm long), which consisted of a 2×8 array of 2.5-cm cube moulds filled with corn kibble, each of the cubes acting as a possible caching site. We attached each tray to the centre of a wooden board (15 cm wide $\times$ 32 cm long) and made it visuospatially unique by attaching an arrangement of Lego bricks along one of the long sides of the tray.

Procedure

All caching trials took place in the subject's home cage. A caching tray was placed on both the left and right hand sides of the cage, and a bowl containing 50 wax worms placed centrally in the cage, equidistant to the trays. This number of wax worms was sufficient to ensure that the jays' caching behaviour was not constrained by the number of items available. Indeed, there were always surplus items left in the food bowl at the end of every trial. Subjects received eight trials in total consisting of four Private trials and four Observed trials in a pseudo-randomized order. During the Private condition we placed solid steel dividers between the cages so that the storers were screened off from their neighbours, whereas in the Observed condition the neighbour's view was not obscured (Fig. 1).

At the end of the 15-min caching period, we removed the trays and food bowl along with any caches made in the subject's home cage. The experimenter then recorded the locations of the food items cached in the trays, and whether the tray was the one nearest to, or furthest from the observer's cage. Screens were then put up, and a retention period of 3 h followed before the trays were returned to the storer's cage, so that the storers could recover their caches in private. During the recovery period, the experimenter recorded the proportion of caches that were recovered, eaten and recached, and where the recached items were hidden. The sites differed as to whether they had been previously used (old sites) or unused (new sites). The trays were then removed and the maintenance diet returned to the home cage.

Data analysis

We recorded the total number of items that remained in the caching trays at the end of the caching trial and took a mean across trials. To compare the number of items cached in the Private and Observed conditions we used a Wilcoxon paired test. Two further Wilcoxon paired tests were conducted to compare the number of items cached in near and far sites in both the Observed and Private condition.

We used proportions when analysing the recovery data, because the values were dependent on the number of items initially cached. We calculated the proportion of cached items that were recovered for each bird, and compared the proportion of caches that were recovered after both the Observed and Private trials, using a Wilcoxon paired test. Upon recovery, items were eaten or recached. We calculated the proportion of caches that were eaten or recached upon recovery, and conducted Wilcoxon paired tests to compare recaching and eating levels in the Observed and Private conditions. The proportion of recached items that were placed in previously used (old) or unused (new) sites was also calculated for each condition.

Mundry & Fischer (1996) suggested that inflated P values can result from the use of modern statistical programs to perform nonparametric statistics on low sample sizes; throughout these experiments we therefore recalculated these tests with a P value close to significance ($0.03 < P < 0.08$) by hand using statistical tables (Siegel & Castellan 1988). All tests were two tailed. Medians and interquartile ranges (IQR) are reported throughout.
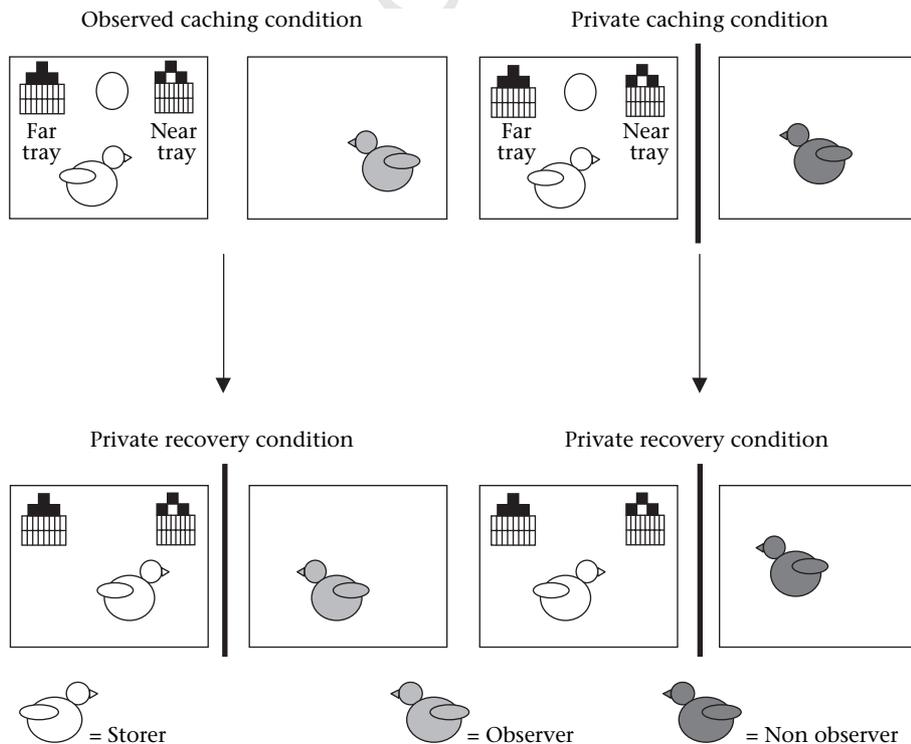
Figure 1. The experimental set-up for both the cache and recovery periods in experiment 1. The dividing line between the cages in the Private conditions represents the opaque screen. The circle represents the food bowl.

Results

Caching

The number of items cached by the birds did not vary across trials in either the Observed (Friedman ANOVA: $\chi_2^2 = 6.0$, $P = 0.09$) or Private condition ($\chi_2^2 = 0.3$, $P = 0.96$). Significantly more items were cached in the Observed (median = 5.6, IQR = 4.4) than in the Private (median = 3.5, IQR = 3.8) condition (Wilcoxon paired test: $T = 4$, $N = 8$, $P = 0.027$). Significantly more items were cached in the far tray in the Observed condition ($T = 4$, $N = 8$, $P = 0.027$), but not in the Private condition ($T = 16$, $N = 8$, $P = 0.67$; Fig. 2).

Recovery

As no effect of trial was detected (Friedman ANOVA: Observed: $\chi_2^2 = 9.8$, $P = 0.08$; Private: $\chi_2^2 = 2.6$, $P = 0.27$), a mean was taken across trials. The proportion of caches recovered by the jays after the Observed (median = 21%, IQR = 36%) and Private (median = 33%, IQR = 31%) conditions was not statistically different (Wilcoxon paired test: $T = 10$, $N = 8$, $P = 0.31$). Furthermore, no statistical differences were detected between the proportion of caches recovered from the near and far trays after either caching condition (Observed: near: median = 37%, IQR = 41%; far: median = 36%, IQR = 41%; Wilcoxon paired test: $T = 13$, $N = 8$, $P = 0.44$; Private: near: median = 20%, IQR = 34%; far: median = 34%, IQR = 45%; $T = 18$, $N = 8$, $P = 0.35$).

In terms of the proportion of cached items that were recovered and eaten, no significant differences were detected between the Observed (median = 29%, IQR = 25%) and Private conditions (median = 18%, IQR = 33%; Wilcoxon paired test: $T = 10$, $N = 8$, $P = 0.29$). Furthermore, the proportion of caches that were recovered and eaten from the near and far trays did not differ significantly in either the Observed (near: median = 11%, IQR = 21%; far: median = 36%, IQR = 41%; $T = 9$, $N = 8$, $P = 0.48$) or Private condition (near: median = 19%, IQR = 36%; far: median = 31%, IQR = 38%; $T = 8$, $N = 8$, $P = 0.15$).

The proportion of a storer's caches that were recached differed significantly with caching condition. Storers recached significantly more items after being observed during caching than when caching took place in private (Wilcoxon paired test: $T = 2$, $N = 8$, $P = 0.02$; Fig. 3). Furthermore, after the Observed condition a significantly higher proportion of caches from the near tray were recached than from the far tray ($T = 2$, $N = 8$, $P = 0.02$). In contrast, no statistical differences were identified in the proportion of caches that were recached from either the near or far tray after the Private condition ($T = 13$, $N = 8$, $P = 0.59$).

When items were recached they could be placed in new or old sites. Unfortunately, a lack of comparable data points meant that a statistical analysis of site use was not possible. However, items recached after the Observed condition were placed exclusively in new sites (100%). In contrast, after caching in private both new (median = 62%, IQR = 24%) and old (median = 38%, IQR = 24%) sites were used.

Discussion

There are three key results from this experiment. First, jays used relative distance from conspecifics when selecting cache sites in the presence of an observer, maximizing the distance between the observer and the cache site. In contrast, when caching occurred in private the jays cached equal amounts in both the near and far sites. Second, storers also cached more items during the Observed condition than in the Private condition (see also Emery et al. 2004). Third, during recovery, the birds then recached those items that were at the greatest risk of being pilfered, namely those that had been cached in the near sites in the presence of the observer. This recaching occurred at the expense of eating those items that had been cached.

As no significant effect of distance was identified, the results of this experiment suggest that jays do use distance as a cache protection strategy. Furthermore, the jays were not simply predisposed to cache far from the observer regardless of social context; the fact that jays did so only during the Observed condition suggests that storers implement a caching strategy that reduces the transfer of visual information to prospective thieves. None the less, the jays
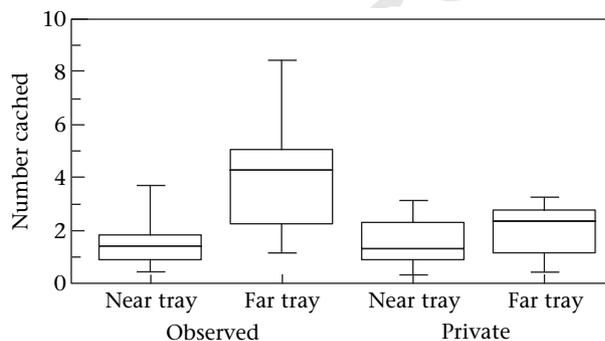
Figure 2. A box and whisker plot of the median number, 25th percentile and 75th percentile of caches that were made in the near and far trays both when the storer was watched by the observer (Observed condition), and when the observer's view was obscured (Private condition) in experiment 1.
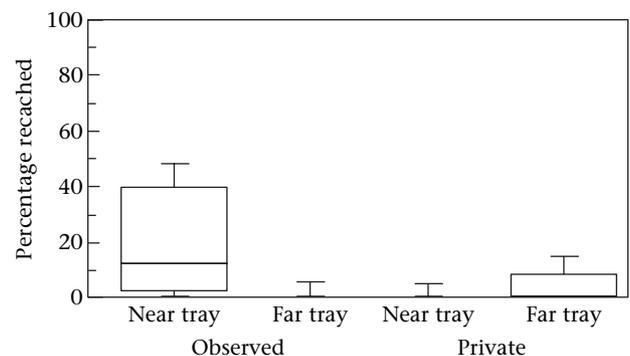
Figure 3. A box and whisker plot of the median percentage, 25th percentile and 75th percentile of caches that were recovered and recached from both the near and far trays after being observed by a conspecific (Observed condition), and after caching unobserved (Private condition) in experiment 1.

did not cache all the items in far sites when observed. One possible reason for this is that an inflexible rule such as 'always cache at the furthest distance possible from conspecifics' would be easy for would-be pilferers to learn. The more unpredictable the placement of caches, the lower the chances of subsequent theft by thieves operating to a standard rule, particularly if storers also compensate for the risk of future cache loss by caching more items when observed. Compensation may be an effective cache protection strategy in this situation because the thieving jays do not usually remove all of the available caches.

Another method for protecting one's caches is to recache any that had been made in the presence of the observer, once the observer has left the scene. The results from this experiment replicated the findings of Emery & Clayton (2001) by showing that recaching levels were highest when the jays had been observed during caching, and that these items were placed largely in new sites. In addition, storers specifically recached items from the near tray in the Observed condition. The observer had greatest visual access to these items, and thus these items were at greatest risk of cache theft. Recaching the high-risk items might be an effective cache protection strategy because the observers would be misinformed about the current cache location.

An alternative explanation for the results we obtained is that storers spent a greater proportion of their time on the far side of the cage in the presence of an observer, whereas they spent their time equally between both sides of their cage when in private. If this were the case, the preference to cache in far sites in the observed condition could be attributed to the storer 'avoiding' their conspecific. Although this account does not explain why the jays preferentially recached items from near sites after being watched during caching, we took the possible effect of conspecific avoidance into account during the next two experiments.

EXPERIMENT 2: EFFECT OF OBSERVER POSITION

Although caching in distant sites reduces the clarity of the visual information available to the observer ('impoverished information'), a more successful tactic may be to prevent the transfer of visual information altogether ('no information'). Our aim in experiment 2 was to establish whether storers are sensitive to the position of the observer, and if so whether they preferentially cache out of sight of the observer when given the opportunity to do so. To establish whether storers preferentially avoided the area of their cage closest to the conspecific, and if so whether or not this preference would be specific to caching, we gave a control trial in which we prevented the bird from caching by providing only noncacheable (powdered) food.

Methods

Subjects and apparatus

The subjects, maintenance, apparatus and housing were as described in experiment 1. However, in this experiment, unlike experiment 1, it was important to verify where the observer was in relation to the storer at the point of caching. As the presence of an experimenter reduces caching rates, a Sony DCR-PC8E digital handycam was positioned approximately 30 cm from the front of the storer's home cage, and used to record the storer's behaviour throughout the caching period.

Procedure

Four subjects started the experiment as storers and four as observers, each bird swapping roles on alternate trials. We conducted 10 trials: five control trials and five test trials. Trials were administered in a counterbalanced order such that on a single day two birds received test trials and two birds control trials. During control trials, each caching tray was covered with two Perspex strips that prevented access to the caching sites, and the food bowl contained powdered nuts to prevent the birds from caching. In test trials the Perspex strips were absent to enable caching, and the food bowl contained 50 wax worms. In the first three test and control trials the cages of both the storers and the observers were partially divided with solid steel dividers (91 × 14 cm), restricting the visual access of both birds to one side of the opposing cage (Free condition, Fig. 4a). In comparison, on the last two trials of each type the storer's cage was partially divided whereas the observer's cage was fully divided; thus the observer was contained on one side (right and left being counterbalanced across test and control trials) and had visual access only to the opposing side of the storer's cage (Constrained condition, Fig. 4b).

At the onset of a caching period we placed two caching trays in the storer's cage, one either side of the barrier, along with a food bowl equidistant to either caching tray. This arrangement meant that the observer had visual access to a caching tray only when on that side of the cage. Consequently, in-view sites were nearer to the observer than the out-of-view sites. The jays were allowed to eat and/or cache freely for 15 min in the presence of an observing conspecific. At the end of the caching period, we removed the trays and food bowl along with any caches made in the storer's cage. The experimenter then recorded the locations of the food items cached in either tray, and the number of caches made in the home cage. Opaque dividers were then put up, and a retention period of 3 h followed. All trays were then returned to the storer's cage in their original location and the storers given a 5-min recovery period. During this time, the experimenter recorded the number of caches recovered and whether these were eaten or recached. The placement of recached items into new (previously unused) or old (used) sites was also recorded. The trays were then removed and the maintenance diet returned.

Video analysis

We scored three variables from the videotapes of each caching trial. First, in the Free condition the sites had to be scored as to whether or not the observer had seen the caching event. Unlike the Constrained condition, near and seen sites and far and unseen sites were not determined by the position of the observer at the beginning
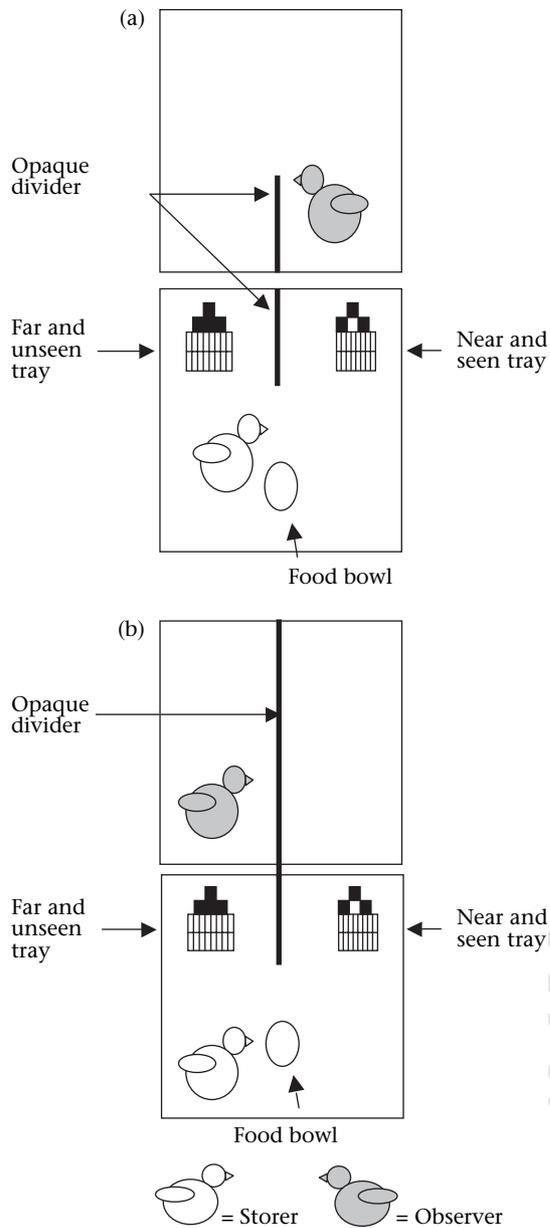
Figure 4. (a) The experimental set-up for the Free condition in experiment 2. The cages of both the storer and observer were partially divided with opaque screens, which restricted the visual access of both birds to one side of the opposite cage. Recovery took place in private (solid divider attached to both sides of the storer's cage). (b) The experimental set-up for the Constrained caching condition in experiment 2. The storer's cage was partially divided, and the observer's cage fully divided, with opaque screens. The observer had visual access to only one side of the storer's cage. Recovery took place in private (solid divider attached to both sides of the storer's cage).

of the trial, because the ability of the observer to move around the cage in the Free condition meant that it could be in view of the storer one second, and out of view the next. As such, the videos for the Free condition were observed by the experimenter and confirmed by another person blind to which site was near. There was a 100% rate of agreement in the score rates. A cache site was scored as

near and seen if the storer had cached in that site while the observer was in view, and as far and unseen if it had not. This meant that it was possible for the status of a cache site to change. For example, if the storer cached in a specific site while the observer was out of view it would be scored as far and unseen; however, if the storer subsequently cached in the same site when the observer was in view the site and its contents would be rescored as near and seen. The observer never appeared to be between sides of the cage during a caching event; thus a site was considered near and seen if the observer was on the same side of the cage as the storer, and far and unseen if it was not.

The second variable to be scored from the tapes was cache movement. Cached items were often moved from one cache site to another during a trial. The total number of times each bird moved each cached item from near and seen or far and unseen sites was recorded for both the Constrained and Free conditions. The total number of times each cache was moved was then summed to give the total number of cache movements by each bird on each trial. Dividing the total number of cache movements by the total number of items that were cached allowed us to analyse the mean number of times items were moved by each bird on each trial. We also recorded whether items were placed in new (unused) or old (used) sites. Finally, the time spent in view and out of view of the observer was recorded for test and control trials in both the Free and Constrained conditions. During the Constrained condition the time spent in view and out of view was determined by the time spent by the storer on either side of the cage, as one side was constantly in view and one out of view. In contrast, in the Free condition the movement of both the storer and the observer determined how much time was spent either in view or out of view.

Data analysis

We calculated the mean number of items cached across trials for each bird in both the Free and Constrained conditions. Wilcoxon paired tests were then conducted to compare the number of items cached in each condition, and the number of items cached in near and seen sites and far and unseen sites within each condition. We also used Wilcoxon paired tests to analyse the mean proportion of cache sites in both the Free and Constrained conditions from which items were moved during trials, and the mean and total number of times each bird moved cached items across trials. In the Free condition, we conducted a further test to compare the average number of times an item was moved from near and seen sites and far and unseen sites.

The time the storer spent in view of the observer on test and control trials was analysed with Wilcoxon paired tests for both the Free and Constrained conditions, as was the proportion of time they spent out of view. We also calculated the rate at which items were cached in near and seen and far and unseen sites for both conditions by dividing the number of items cached in near and seen or far and unseen sites by the time spent in view and out of view of the observer, respectively. Wilcoxon paired tests were then used to compare the caching rates in near and

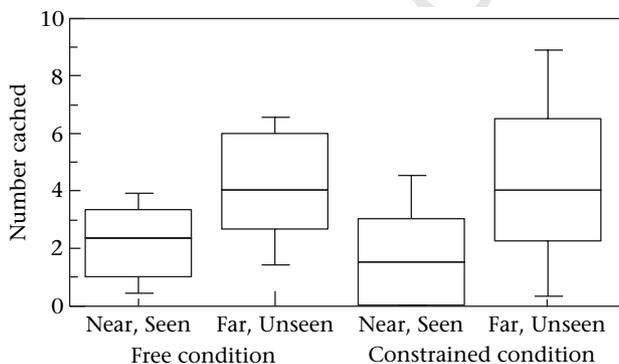seen and far and unseen sites in both the Free and Constrained conditions.

The recovery data were analysed as in experiment 1. As caching trials were statistically similar, we recorded the total number of items that remained in near and seen and far and unseen sites at the end of the caching trial and took a mean across trials. As in the previous experiment, alpha was set at 0.05 and those results with a P value close to the alpha value for significance ($0.03 < P < 0.05$) were recalculated by hand.

Results

Caching

There was no effect of trial on the number of items cached for both the Free (Friedman ANOVA: $\chi^2_2 = 0.2$, $P = 0.91$) and the Constrained (Wilcoxon paired test: $T = 15$, $N = 8$, $P = 0.90$) conditions. The number of items the jays cached was similar in both the Constrained (median = 6, IQR = 3.6) and Free conditions (median = 5.5, IQR = 5.5; $T = 15$, $N = 8$, $P > 0.99$). However, in the Constrained condition storers cached significantly more items in far and unseen sites than in near and seen sites ($T = 4$, $N = 8$, $P = 0.027$; Fig. 5). A preference for far and unseen sites was also identified in the Free condition, although it did not reach statistical significance ($T = 7$, $N = 8$, $P = 0.07$).

During each trial, the jays spent time on either side of the home cage. They appeared to spend their time equally in view and out of view of the observer regardless of condition or trial type (Table 1). Indeed, no statistical differences were detected in the time spent in view of the observer on test and control trials in either the Free (Wilcoxon's paired test: $T = 8$, $N = 8$, $P = 0.78$) or Constrained condition ($T = 11$, $N = 8$, $P = 0.33$). This pattern of results was reflected in the analysis of the time spent out of view of the observer during both trial types, which also failed to identify any statistical differences in storer position (Free condition: $T = 8$, $N = 8$, $P = 0.33$; Constrained condition: $T = 11$, $N = 8$, $P = 0.33$).

Table 1. The median time and interquartile range (IQR) that the storer spent in view and out of view of the observer on test and control trials for both the Constrained and Free conditions of experiment 2
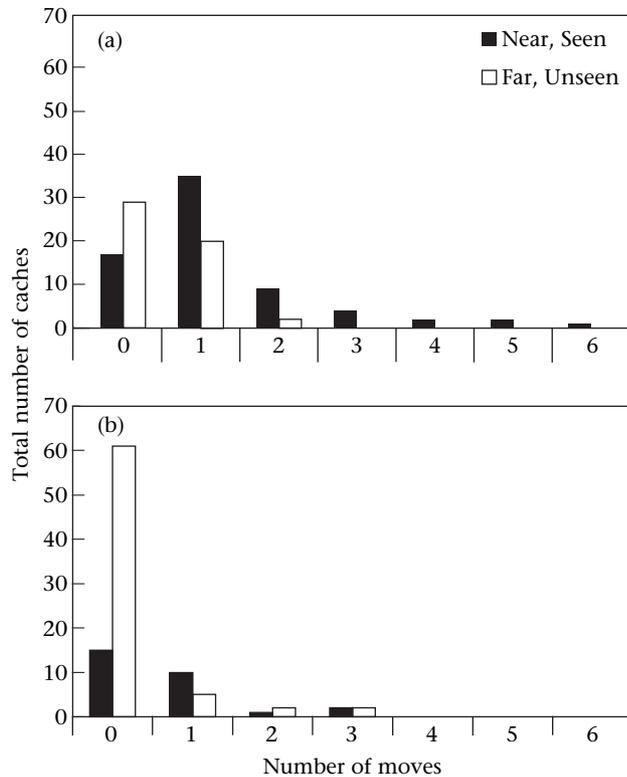
Trial type	In view		Out of view	
	Median	IQR	Median	IQR
Free condition				
Test	6.4	6.1	8.6	6.1
Control	10.4	7.4	4.6	7.4
Constrained condition				
Test	8.8	4.0	6.2	4.0
Control	7.9	3.6	7.1	4.1

The observer had visual access to only one side of the storer's cage in the Constrained condition and to both sides in the Free condition.

The jays cached at comparable rates (number of items cached/min) in both the Free (0.4 items/min, IQR = 0.3) and Constrained (median = 0.4 items/min, IQR = 0.4) conditions (Wilcoxon paired test: $T = 17$, $N = 8$, $P > 0.99$). A detailed analysis revealed that the birds cached at a statistically higher rate in far and unseen sites (Free: median = 0.3 items/min, IQR = 0.2; Constrained: median = 0.3 items/min, IQR = 0.3) than in near and seen sites (Free: median = 0.2 items/min, IQR = 0.1; Constrained: median = 0.1 items/min, IQR = 0.2) in both the Free ($T = 5$, $N = 8$, $P < 0.05$) and Constrained conditions ($T = 5$, $N = 8$, $P < 0.05$). During the caching phase of the experiment, a food item was often cached and then moved to a new site. Each item was moved up to six times during a caching phase. Items were not moved from every cache site: the proportion of sites containing caches from which items were moved was higher in the Free condition (median = 67%, IQR = 33%) than in the Constrained condition (median = 33%, IQR = 34%; $T = 2$, $N = 8$, $P = 0.02$). Caches were moved significantly more times during the Free condition than in the Constrained condition ($T = 2$, $N = 8$, $P = 0.01$; Fig. 6). The mean number of times a cache was moved was also significantly higher in the Free condition (median = 1.3, IQR = 0.88) than in the Constrained condition (median = 0.3, IQR = 0.4; $T = 2$, $N = 8$, $P = 0.01$).

The number of times items were moved in the Constrained condition was too low to allow further analysis. However, items from near and seen sites were moved significantly more times than those from far and unseen sites (near and seen: median = 1.2, IQR = 0.9; far and unseen: median = 0.2, IQR = 0.4; Wilcoxon paired test: $T = 2$, $N = 8$, $P = 0.01$; Fig. 6a).

When caches were moved they could be placed in new or old sites. The low level of cache movement in the Constrained condition (four birds) meant that a statistical analysis of new and old site use was not possible. This was also the case for the number of items from far and unseen sites in the Free condition, but an analysis of items moved from near and seen sites in the Free condition revealed no statistical preference for either site type (new: median = 67%, IQR = 70%; old: median = 45%, IQR = 31%; Wilcoxon paired test: $T = 12$, $N = 8$, $P = 0.48$).

Figure 5. A box and whisker plot showing the median number, 25th percentile and 75th percentile of items cached in near and seen or far and unseen sites, both when the observer had visual access to only (Constrained condition) or potentially both (Free condition) sides of the storer's cage in experiment 2.

Figure 6. (a) The total number of times individual caches from near and seen and far and unseen sites were moved during the Free condition of experiment 2. In this condition, opaque screens prevented the observed having visual access to both sides of the storer's cage at any one time. (b) The total number of times individual caches from near and seen and far and unseen sites were moved during experiment 2, when the observer was able to see only one side of the storer's cage (Constrained condition).

Recovery

There was no statistical difference in the number of probes that storers made before recovering a cache that had or had not been moved from the seen sites in the Free condition (moved: median = 2.0, IQR = 1.3; unmoved: median = 3.5, IQR = 2.3; Wilcoxon paired test: $T = 10$, $N = 8$, $P = 0.23$). After the Free caching condition, the jays recovered a median of 34% of their caches (IQR = 29%), in comparison to 22% (IQR = 18%) after the Constrained condition (Wilcoxon paired test: $T = 10$, $N = 8$, $P = 0.20$). Upon recovery, items were either eaten or recached. No statistical differences were detected in the proportion of items that were recovered and eaten from near and seen sites and far and unseen sites in either the Constrained ($T = 12$, $N = 8$, $P = 0.83$) or Free condition ($T = 11$, $N = 8$, $P = 0.50$).

It was not possible to analyse whether recached items were those that had been cached in near and seen or far and unseen sites. Indeed, in the Constrained condition no recaching occurred. In the Free condition only three birds recached. Although the proportion of caches these birds recached was extremely low (median = 2%, IQR = 8%), recached items were taken exclusively from near and seen sites, and were placed only in new sites. Note also that this recaching behaviour differs from the

moving of caches seen during caching, in that the items were moved only to one new site, as opposed to being moved multiple times.

Discussion

There are two main results in this experiment. The first is that scrub-jays preferred to cache in the far and unseen sites in both the Free and Constrained conditions. Second, the jays would often move a cached item multiple times within the caching phase, and this happened much more frequently in the Free condition. It is worth emphasizing here the difference between the Free and Constrained conditions. In the Constrained condition the location of the observer in relation to cache sites was reliable, one tray being constantly near and seen and one constantly far and unseen. In contrast, in the Free condition whether sites were near and seen or far and unseen depended on the observer's position. Furthermore, the ability of the observer to move freely within its cage meant that its position was uncertain. Perhaps it is this uncertainty that led to the implementation of an additional cache protection strategy, namely moving the caches around multiple times during the caching phase.

Note also that it was the items that were cached in view of the observer that were moved around multiple times, compared to those cached in sites that the observer could not see. Unlike recaching at recovery, there was no preference for placing these items in new sites. Presumably, the aim of repeatedly moving caches in the presence of potential pilferers is rather different from the aim of recaching an item when in private during recovery. The principal benefit of recaching during recovery is that the item is moved from a cache site that the observer knows about to a new site of which the observer is ignorant (Emery & Clayton 2001). In contrast, the repeated movement of caches during caching is more likely to confuse those onlookers, and thus new and old cache sites may be treated alike.

Indeed, we suggest that moving items around during caching may function as a 'confusion' tactic. If the end location of caches becomes less certain, then the accuracy with which observers pilfer cache sites should be reduced. One potential cost of implementing a confusion tactic during caching is that the accuracy with which storers recover their own caches is reduced. This may occur because the memory for each new cache site would suffer from interference from the memory of old cache sites. The number of times a bird probes various cache sites before recovering a cache is used as an index of memory performance (Clayton & Dickinson 1998). However, we found no statistical difference in the storer's cache recovery accuracy, as moved and unmoved caches were recovered with equal precision. It would have been interesting to have allowed the observers access to the storer's cache sites, and to have monitored whether the accuracy with which they pilfered moved and unmoved items differed. Unfortunately, however, this would have made it difficult in subsequent trials to determine whether specific cache sites were avoided as part of a cache protection strategy.

For example, if items were pilfered specifically from near and seen sites, it would not be possible to tell whether differential reinforcement or the use of a cache protection strategy was the reason for the low level at which they were used during caching.

For the Free condition, the recovery behaviour of the jays followed the predicted pattern, namely that items cached in view of the observer were selectively reached, and specifically into new sites. As discussed previously, this results in observers being misinformed as to the current location of cache sites. The proportion of caches that were reached was, however, much lower in this experiment than in the previous one. One possible reason for the reduction in levels of reaching might be that items were moved multiple times during caching. Both caching in sites that observers cannot see and moving ones they have seen to new places result in the potential thief being either ignorant of the cache location, or at least uncertain, making further cache protection strategies redundant. It was surprising, however, that recovery levels were so low after caching in the Constrained condition, and that no items were reached. This may result from the high level of certainty about the safety of the caches that stems from caching in sites that are constantly out of view.

Taken together, the results of this experiment showed that scrub-jays appear to use cache protection strategies to reduce or prevent the transfer of visual information about a caching event to an observer. This is demonstrated by the preference to cache in sites that observers cannot see and by the propensity repeatedly to move items cached in the observer's visual range. The dominant use of far and unseen cache sites cannot be attributed to a preference for solitude by the storer, as there was no significant difference in the time spent in or out of view of the observer. However, the position of the trays relative to the observer was confounded with distance. Throughout the experiment, the out-of-view sites were consistently slightly further away from the observer than in-view sites. This meant that it was possible to use the rule 'cache in sites that the observer cannot see', but also to use the rule 'cache in sites that are furthest from the observer', and that it was not possible to tell which of the two caching strategies was being used. Furthermore, although both strategies would represent successful tactics, it is not yet clear whether the birds differentiate between what the observer could see during caching and what they the storers could see.

EXPERIMENT 3: CACHING OUT OF VIEW

The final experiment tested whether jays would preferentially cache in sites that observers could not see, when it was not possible to use distance as a protection strategy (as in experiment 2). In this experiment both in-view and out-of-view sites were equidistant to the observer, and the jays were also able to cache in private. As in the previous experiment, to ensure that any preference for caching in view or out of view of the observer could not be ascribed to a fear of the open or the conspecific, we gave a control trial with powdered food to prevent the birds from caching.

Methods

Subjects, apparatus and procedure

The housing, subjects, apparatus and cage set-up were the same as in the Constrained condition of experiment 2 in all but two respects. First, the observing birds were restricted to one half of their home cage by means of a steel divider (91 × 76 cm), and this section of the observer's cage was located centrally to the storer's cage (Fig. 7). Second, a solid steel divider (91 × 46 cm) was attached to one side of the back of the storer's cage (left and right sides being counterbalanced across subjects), restricting the observer's view to the opposing side.

Four jays began the experiment as storers and four as observers, switching roles after each trial. Each jay underwent a single test and control trial (as in experiment 2) both when observed and when in private (on Private trials a second steel divider [91 × 46 cm] was attached to the back of the storer's cage to prevent the observer from seeing the caching event). Trials were given in a counterbalanced order, such that on each day no two birds were given the same trial type (Private test trial, Private control trial, Observed test trial, Observed control trial). The experimental procedure was identical to that of the Constrained condition of experiment 2.

Video analysis

We scored the videos in the same manner as for the Constrained condition of experiment 2. Whether potential caching sites were in view or out of view of the observer was determined by the observer's position at the start of the trial. We recorded the number of times caches were moved during each trial for both Observed and Private conditions. In the Observed condition we also recorded whether moved items were in view or out of view. The only other variable scored from the tapes was how long each storer spent in view and out of view of the observer
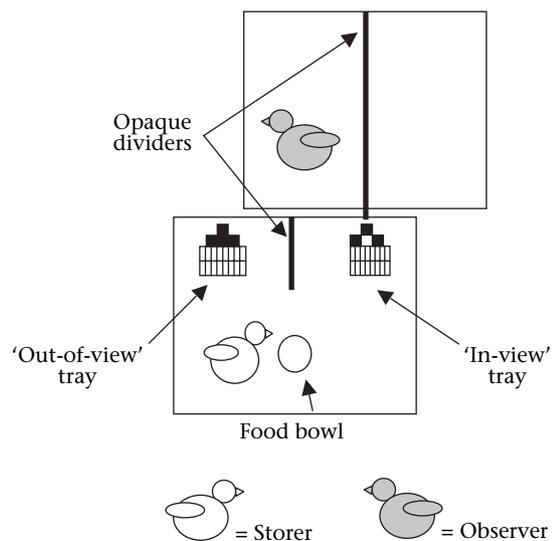
Figure 7. The experimental set-up for the caching condition in experiment 3. Recovery took place unobserved (solid divider attached to both sides of the storer's cage).

during both test and control trials in both the Observed and Private conditions.

Data analysis

The number of items that were cached was analysed with a Friedman ANOVA with site type as a within-subject variable (in view, out of view, mean of Private trays). We analysed the mean proportion of caches moved during trials for both conditions, along with the average and total number of times a bird moved items across trials. In the Observed condition, a Wilcoxon paired test was conducted to compare the average number of times an item was moved from in-view and out-of-view sites. We also used Wilcoxon paired tests to analyse the time spent by the storer both in view and out of view of the observer on test and control trials and the rate at which items were cached in both conditions. We calculated the latter rate by dividing the number of items cached in in-view, out-of-view and Private sites by the time spent on the corresponding side of the cage. A Friedman ANOVA was then conducted to compare the in-view and out-of-view caching rates with the mean Private rate. Dunnett's tests were used to identify the source of any significant interactions. The jays' recovery behaviour was analysed as in experiment 2.

Results

Caching

Although the jays cached a median of 4.5 items (IQR = 4.3) during the Observed test trial and only 1.5 items (IQR = 4.0) during the Private test trial, we were unable to detect a statistically significant difference between the two conditions (Wilcoxon paired test: $T = 7$, $N = 8$, NS). However, there was a significant difference between the number of items the jays cached in the out-of-view tray, in-view tray and the mean of the Private trays (Friedman ANOVA: $\chi_2^2 = 2.57$, $P = 0.03$; Fig. 8). Upon further analysis, we found that the birds cached significantly more items in the out-of-view tray than in both the in-view tray (Dunnett's test: $q = 2.9$, $N = 8$, $P < 0.05$) and the mean of the Private trays ($q = 4.1$, $N = 7$, $P < 0.01$). Importantly, however, no statistical difference was identified between the number of items cached in the in-view tray and the mean of the Private trays ($q = 1.2$, $N = 7$, NS).

During a trial the jays spent time on both sides of the home cage. They appeared to spend their time equally both in view and out of view of the observer regardless of condition or trial type (Table 2). No statistical differences were detected in the time spent in view (Wilcoxon paired test: $T = 15$, $N = 8$, $P = 0.67$) or out of view of the observer ($T = 15$, $N = 8$, $P = 0.67$) during the test and control trials of the Observed condition. Furthermore, there were no differences in the time the jays spent on either the left ($T = 14$, $N = 8$, $P = 0.61$) or right side of their cage ($T = 15$, $N = 8$, $P = 0.67$) during either trial type in the Private condition.

We conducted a Friedman ANOVA to compare the rate at which items were cached (items cached/min) in the in-view and out-of-view trays during the Observed condition
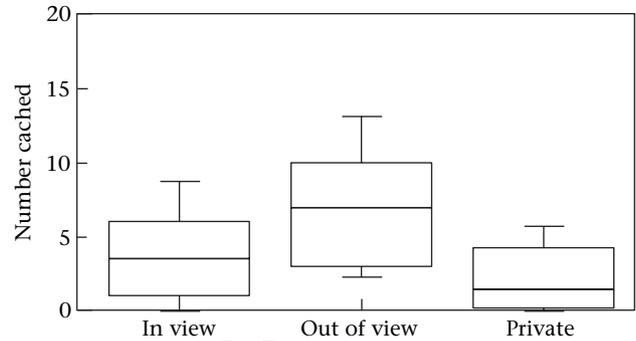
Figure 8. A box and whisker plot showing the median number, 25th percentile and 75th percentile of items cached in both the in-view and out-of-view trays when watched by a conspecific (Observed condition), and the mean number of items cached when not observed (Private condition) in experiment 3.

with the mean of the Private trays (Friedman ANOVA: $\chi_2^2 = 9.8$, $P = 0.01$). A post hoc comparison revealed that this difference was caused by a significantly higher rate of caching in the out-of-view tray when observed (median = 1.5 items/min, IQR = 1.7) than in the in-view tray in the same condition (median = 0.4 items/min, IQR = 0.6; Dunnett's test: $q = 2.9$, $N = 8$, $P < 0.05$) and the mean caching rate of the Private condition (median = 0.3 items/min, IQR = 0.5; $q = 3.6$, $N = 8$, $P < 0.05$). In contrast, no statistical difference was identified between the rate of caching between the in-view tray and the mean rate of caching in the Private trays ($q = 1.0$, $N = 8$, NS).

During the Private condition three birds did not cache, so we could not make a statistical comparison between the number of times caches were moved in private (total: median = 6.9, IQR = 6.3; mean: median = 0.67, IQR = 0.7) and when observed (total: median = 5.2, IQR = 3.7; mean: median = 0.6, IQR = 0.7). During the Observed condition, the total number of times items from the in-view (median = 3.0, IQR = 4.5) and out-of-view (median = 2.2, IQR = 2.5) trays were moved was statistically similar (Wilcoxon paired test: $T = 11$, $N = 8$, $P = 0.39$). The mean number of times an item was moved

Table 2. The median time and interquartile range (IQR) that the storer spent in view and out of view of the observer on test and control trials for both the Observed and Private conditions of experiment 3

Trial type	In view		Out of view	
	Median	IQR	Median	IQR
Observed condition				
Test	8.9	5.2	6.0	5.2
Control	8.4	9.0	6.7	9.0
Private condition				
Test	6.8	11.7	8.2	11.7
Control	11.6	11.5	3.4	11.5

The storer was watched by a conspecific in the Observed condition but was not observed in the Private condition.

from both the in-view (median = 0.6, IQR = 0.7) and out-of-view trays was also comparable (median = 0.6, IQR = 0.7; $T = 11$, $N = 8$, $P = 0.31$). When items were moved they could be placed in new or old sites. The proportion of new sites used was similar for both the in-view (median = 88%, IQR = 60%) and out-of-view trays (median = 86%, IQR = 60%; $T = 17$, $N = 8$, $P > 0.99$), as was the proportion of old sites (in view: median = 13%, IQR = 60%; out of view: median = 39%, IQR = 85%; $T = 13$, $N = 8$, $P = 0.46$).

Recovery

Since only four birds recovered in-view caches, three birds out-of-view caches and two birds Private caches, a statistical analysis of the proportion of items recovered and then eaten or recached was not feasible. During the Private condition items were recovered and eaten from both trays (median = 0%, IQR = 50%) and recaching did not occur. In the Observed condition, the jays recovered a median of 0% (IQR = 8%) of their caches from the out-of-view tray, all of which were eaten. In contrast, the proportion of caches from the in-view tray that were recovered and eaten (median = 0%, IQR = 10%) was somewhat lower than those that were recovered and recached (median = 12%, IQR = 35%). In each instance of recaching from the in-view tray, items were placed specifically in new sites.

Discussion

There are three key results from this experiment. First, in the presence of a conspecific the scrub-jays cached predominantly in sites that observers could not see, even though the confound of distance had been removed. In contrast, when caching occurred in private the jays cached equal amounts in both trays. Second, few items were moved around during caching. On the occasions that items were moved they were taken equally from the in-view and out-of-view trays. Similarly to the Constrained condition of experiment 2, the absence of a 'confusion' tactic appears to result from the predictability of the observer's position, and the constancy with which they could or could not see potential cache sites. Finally, upon recovery, the jays restricted their recaching behaviour to specifically high-risk items, those cached in the in-view tray after the Observed condition. By doing so, those items at the greatest risk of cache theft were provided with a degree of protection, as observers were misinformed of the current location of caches.

As only a single trial was given, the preference for caching in the out-of-view tray could not be explained by differential reinforcement, nor could it be ascribed to a distance rule, as both caching trays were equidistant from the observer. Furthermore, video analysis ruled out the possibility that increased caching in the out-of-view tray was due to a preference for solitude, and so was a by-product of the different times spent in either section of the home cage. Any relation between caching patterns and a conspecific avoidance strategy can be further discounted, because the rate at which the jays cached

during the Private condition was statistically similar to the rate of caching in the in-view tray. If solitude were a motivating factor behind increased caching rates, we would have expected caching levels during the Private condition to have been statistically similar to the out-of-view tray and significantly higher than the in-view tray. There was an overall trend, however, although not statistically significant, to do the opposite. The amount that storers cached in the Observed condition was somewhat higher than in the Private condition. The implementation of this compensatory strategy was seen previously in experiment 1 where all sites were in view of the observer. In the current experiment, however, the jays cached mainly in out-of-view sites; therefore further cache protection strategies such as compensation initially appear unnecessary. Yet although the observer could not see the second caching tray, they could see the storer carrying food items elsewhere. The observer may then have inferred that the storer was caching without possessing information on the precise location of the cache sites; in this situation a compensatory strategy to protect against naïve search would be advantageous.

GENERAL DISCUSSION

These three experiments show that scrub-jays use multiple strategies to minimize cache theft from observing conspecifics, during both caching and recovery. Caching out of view of conspecifics may be one of the safest tactics because it prevents conspecifics from observing the caching event, and removes the need for further cache protection strategies. The jays, however, have demonstrated the ability to use several other strategies when caching out of view is not a viable option (Table 3).

While it may not be possible to prohibit visual access to a caching event, it may be possible to reduce the clarity of the information transferred to observers. This appears to be an integral part of a corvid's caching strategy. For example, in the field, storing birds tend to cover their caches either with the caching substrate or with locally available material such as stones and leaves. This then protects those caches against potential thieves, which might otherwise have been able to locate those sites visually and pilfer them. Indeed, in these experiments the jays generally redistributed the caching substrate after each caching event; this meant that even used sites looked undisturbed. It was therefore often the case that we were unable to tell by looking whether or not the jays had even used the caching trays. In the distance experiment the sites that were used were those furthest from the observer, a tactic identified in several other avian species (Clarkson et al 1986; Waite 1992; Lahti et al. 1998). By caching predominantly in far sites the visual information available to the potential thief becomes impoverished, with the possible consequence that their pilfering accuracy is reduced. Yet this is not the only way to impoverish visual information. For example, in an experiment where the jays could cache in 'shady' or 'well-lit' sites, 'shady' sites were chosen in the presence of an observer, whereas both sites were used equally in their absence (Dally et al. 2004).

Table 3. Summary of the cache protection strategies used in each experiment

Strategy	Definition	Experiment 1 Distance	Experiment 2 Observer position	Experiment 3 In and out of view
Compensation	Cache more (to offset predicted loss)	Yes	No	No
Confusion	Move caches around repeatedly	N/A	Yes	No
Impoverished information	Cache in hard-to-see sites	Yes	No	No
No information	Cache out of view	N/A	Yes	Yes
Misinformation	During recovery move (specifically high-risk) items to new sites	Yes	Yes	Yes

N/A: Not applicable.

The preference for the storers to cache out of view of observers raises the possibility that they understand what others can and cannot see. However, it is not yet clear whether this is the case, or whether, at a cognitively less complex level, these sites are preferred because the observer is perceived to be absent at the moment of caching ('out of sight, out of mind'). In contrast, the propensity to reduce visual information by caching in 'far' or 'shady' sights cannot be explained in this manner. These sites are used differentially even though the observer is constantly in view. It may still be feasible, however, to explain this site use in terms of the storer's visual perspective. If these sites are harder for the observer to see, it is automatically harder for the storer to see the observer.

Cache protection strategies were also used that had no effect on the quality of visual information available to the observer, and these were tactics often implemented in combination with a second visual strategy. For example, in the distance experiment the jays used a compensatory tactic in conjunction with the distance strategy (Table 3). This tendency to increase the rate of caching in the presence of an observer has been identified in other species (Bossema 1979; Emery et al. 2004), and may act towards offsetting the predetermined risk of cache loss through pilfering. Yet this tactic should be nonpreferred, being both energetically costly and providing no visual protection to the location of the cache sites. These factors may explain both its absence when it is possible to cache out of view of observers and the fact that it was used in conjunction with, not instead of, another tactic.

Furthermore, if observers are not stationary it may not be possible to cache out of view. This situation was presented in the Free condition of experiment 2. In response to the unpredictable location of the observers, the storers made cache location unpredictable, repeatedly moving around items that observers had seen to be cached. By moving caches in an unpredictable manner, their final position may be less clear to an observer than if they were left in their original cache site. The potential cost to the storer in terms of interference effects proved not to be significant, as items that were moved around were recovered with the same level of accuracy as those that were left in their original cache site. This suggests that the storers update their memory as to the cache's new position. It remains to be seen, however, whether observers can do the same.

In every experiment a few items were cached in nonpreferred sites ('near', 'near and seen', 'in view'; Table 3).

There may be an advantage in not hiding all one's caches in one place, because unpredictability might provide the best insurance against pilfering. Caching some items in view of the observer may act to focus the competitor's attention away from other caches and thus increase the protection of the majority. This may be especially true in this experimental set-up because, although it could not always see both caching sites, the observer may have inferred the onset of caching elsewhere as the storer often moved out of view while in possession of food items.

The one cache protection strategy that was apparent in all three experiments was recaching ('misinformation'; Table 3). The low level of recaching in the last two experiments might have been the by-product of the ability to cache in sites unseen by the observer. If potential thieves are uninformed about the location of cache sites, a cache protection strategy aimed to misinform becomes redundant. This assumption is supported by the fact that when recaching did occur, it was specifically directed at high-risk items, those items that had been cached in view of the observer. These items, as expected, were consistently placed in new sites and observers were therefore misinformed as to the current location of cached items.

At present the ability to understand what others can and cannot see and to attribute knowledge states appears to be restricted to the great apes (Kummer et al. 1996; Hare et al. 2000; but see Karin-D'Arcy & Povinelli 2002). However, our findings raise the intriguing possibility that scrub-jays may also be capable of complex social cognition given that they use a number of cache protection strategies to confuse and reduce the visual information available to observers. Studies have suggested that these birds possess elements of mental time travel (Clayton & Dickinson 1998; Clayton et al. 2003), experience projection and possibly even knowledge attribution (Emery & Clayton 2001). Taken together such results may provide the converging evidence for 'triangulation' suggested by Heyes (1993) for the possession of 'theory of mind' in animals.

Acknowledgments

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