Anim Cogn (2004) 7 : 37–43
DOI 10.1007/s10071-003-0178-7

ORIGINAL ARTICLE

Nathan J. Emery · Joanna M. Dally · Nicola S. Clayton

Western scrub-jays (*Aphelocoma californica*) use cognitive strategies to protect their caches from thieving conspecifics

Received: 23 November 2002 / Revised: 28 April 2003 / Accepted: 14 May 2003 / Published online: 26 June 2003
© Springer-Verlag 2003

Abstract Food caching birds hide food and recover the caches when supplies are less abundant. There is, however, a risk to this strategy because the caches are susceptible to pilfering by others. Corvids use a number of different strategies to reduce possible cache theft. Scrub-jays with previous experience of pilfering other's caches cached worms in two visuospatially distinct caching trays either in private or in the presence of a conspecific. When these storers had cached in private, they subsequently observed both trays out of reach of a conspecific. When these storers had cached in the presence of a conspecific, they subsequently watched the observer pilfering from one of the trays while the other tray was placed in full view, but out of reach. The storers were then allowed to recover the remaining caches 3 h later. Jays cached more worms when they were observed during caching. At the time of recovery, they re-cached more than if they had cached in private, selectively re-caching outside of the trays in sites unbeknown to potential thieves. In addition, after a single pilfering trial, the jays switched their recovery strategy from predominantly checking their caches (i.e. returning to a cache site to see whether the food remained there) to predominantly eating them. Re-caching remained constant across the three trials. These results suggest that scrub-jays use flexible, cognitive caching and recovery strategies to aid in reducing potential future pilfering of caches by conspecifics.

Keywords Caching · Cache protection · Corvids · Pilfering · Scrub-jay

Introduction

Many birds and mammals hide food caches for future consumption (Vander Wall 1990), and largely rely on memory to locate these food caches (e.g., Balda and Kamil 1989; Clayton and Dickinson 1998.) There are a number of costs and benefits of storing food in the presence of others. The benefits include increased vigilance and defence against predators (Krebs and Davies 1993), and learning the location of good food sources, so-called information centres (Ward and Zahavi 1973). However, as the number of feeding partners increases, there is a greater chance that another individual will encounter the storer's caches and pilfer them.

Food-stealing or 'kleptoparasitism' occurs, not only between different species (Burnell and Tomback 1985), but also between conspecifics (Brockmann and Barnard 1979; Heinrich and Pepper 1998). Although potential thieves may locate a conspecific's caches by chance, a more accurate method is to rely on observational spatial learning of where the storer cached. Pinyon jays (Bednekoff and Balda 1996a) and Mexican jays (Bednekoff and Balda 1996b), for example, are extremely accurate at locating caches they saw another individual make.

The social context of caching behaviour between storers and stealers can be seen as an 'arms race' with stealers developing new opportunities for social learning, and storers engaging in counter-measures to minimise the risk of having their caches pilfered. In this 'arms race', however, individuals play the roles of both storer and stealer, and so may be required to transfer their experience from one role to another.

Much of the work in this area has been derived from observations of corvids, particularly ravens (*Corvus corax*) in the field. It has been shown that storers will delay caching if other ravens are in the vicinity, and wait until would-be pilferers are distracted or have disappeared before they resume caching (Heinrich and Pepper 1998; Bugnyar and Kotrschal 2002). Both ravens (Heinrich 1999) and Northwestern crows (*Corvus corinius*; James and Verbeek 1983) make false caches in the presence of ob-

N. J. Emery (✉)
Sub-department of Animal Behaviour, University of Cambridge,
High Street, CB3 8AA Madingley, Cambs , UK
Tel.: +44-01223-741811, Fax: +44-01223-741802,
e-mail: nje23@cam.ac.uk

J. M. Dally · N. S. Clayton
Department of Experimental Psychology,
University of Cambridge, Downing Street,
CB2 3EB Cambridge, UK

servers, which are repeatedly moved around, and ravens preferentially store food behind obstacles so that other ravens cannot see where the caches are being made (Bugnyar and Kotrschal 2002). Clarkson (1986; Clarkson et al. 1986) showed that magpies (*Pica pica*) adjusted the density of their caches by spacing them further apart and placing them further away from the central food source if the risk of pilfering was high (see also crows; James and Verbeek 1983). Finally, some corvids return alone to caches they had hidden in the presence of conspecifics, and readily re-cache them in new places (Goodwin 1956; DeGange et al. 1989; Balda and Kamil 1992; Heinrich 1999; Bugnyar and Kotrschal 2001; Emery and Clayton 2001; Robinette Ha et al. 2003).

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. Emery and Clayton (2001) allowed hand-raised western scrub-jays to cache either in private or while a conspecific was watching. Individuals that had prior experience (outside of the experiment) of pilfering another bird's caches subsequently re-cached food in new cache sites, but only when they had been observed during caching. (It should be noted that the birds in the Emery and Clayton, 2001 study did not observe their caches being pilfered and they did not receive any opportunity to pilfer another individual's caches during the course of the experiments.)

By contrast, those without pilfering experience did not do this, even though they had observed the caching behaviour of others. These results suggested that these birds related information about their previous experience as a pilferer to the possibility of future stealing by another individual, and modified their recovery strategy accordingly. This experiment therefore focussed on the counter-strategies of the storer when previously observed by a potential stealer.

The particular caching and recovery strategy used may also depend on whether storers observe a conspecific stealing their caches or whether they discover that some of their caches have been pilfered when they come to recover them (such as when taken by an experimenter). In the latter case, Baker and Anderson (1995) found that black-capped chickadees that had half of their caches stolen by experimenters did not cease caching in the once pilfered sites when they were given new seeds to cache. This result contrasts with an earlier study by Hampton and Sherry (1994) that found that black-capped chickadees responded to systematic cache loss between caching and recovery by avoiding caching in once pilfered sites.

The only previous study to examine the effects of observing caches being stolen between caching and recovery was in Merriam's kangaroo rat, a solitary rodent that usually scatter-hoards caches throughout their territory (Preston and Jacobs 2001). Whether or not the rat was observed during caching had little effect on the amount cached (or subsequent caching behaviour), however, if the storer had observed its caches being stolen by a conspecific, it switched from scatter- to larder-hoarding in its home cage, where their caches could be easily defended.

For the present study, we therefore investigated the caching and recovery behaviour used by scrub-jays if they observed a conspecific stealing some of their caches, which that conspecific had previously seen being cached, and what they would do with any remaining caches that were returned to them. Based on our previous study, we predicted that the scrub-jays would re-cache, specifically in new sites, if they had been observed during caching, possibly choosing cache sites that were easily defended and inaccessible to potential thieves. We also predicted that the birds would show a preference for recovering those caches most at risk from potential pilfering in the future (i.e. those caches remaining close to the pilfered cache sites, in the pilfered tray).

Methods

Subjects

Sixteen sexually mature hand-raised western scrub-jays (*Aphelocoma californica*) of mixed-sex were used during the experiment. The birds were individually housed in steel cages (width: 91 cm, height: 76 cm, length: 76 cm) and had previously participated in a number of cognitive experiments on episodic-like memory (Clayton and Dickinson 1998, 1999; Clayton et al. 2001b) and social cognition (Emery and Clayton 2001). The birds were maintained on a 10:14 h light:dark cycle, with a diet of ad libitum powdered nuts, mixed seeds, whole peanuts, sunflower seeds, dog biscuits, ox heart, egg, grapes, and water, with additional mealworms and wax worms.

Eight scrub-jays (taken from the O+P and P groups from Emery and Clayton 2001) had previous experience of stealing the caches of conspecifics. These birds comprised the storer group in the present study. An additional eight scrub-jays, which had no previous experience of pilfering another's caches [the original O group from Emery and Clayton 2001 plus an additional bird not used in the Emery and Clayton (2001) study], comprised the pilferer group in the present study.

Apparatus

All caching trials were performed in the subject's home cage. For each trial (*n*=3 for each condition, total *n*=6), jays were presented with a 15-cm bowl of wax worms and two visuospatially distinct caching trays. The caching trays were constructed from ice cube trays (width: 6 cm, length: 25 cm) attached to a wooden board (width: 15 cm, length: 32 cm), with a unique construction of Lego Duplo bricks attached alongside one side of the ice cube tray. Each tray contained a 2×8 array of 2.5 cm moulds, filled with powdered corn kibble, which presented 16 possible cache sites per tray.

Procedure

During caching, a bowl containing 50 wax worms was placed in the centre of the cage and each caching tray was placed at either end of the subject's home cage. Storers received three in-private trials in which they cached for 15 min with no observer watching. The storer's privacy was assured as a black curtain was attached to the subject's cage, and solid steel cage dividers prevented next-door-neighbours from observing caching. Storers also received three observed trials in which they were allowed to cache whilst being observed by one individual from the pilferer group. Trial or-

Table 1 Cache, recovery and re-caching location definitions

Behaviour	Definition
Caching	Individual places the worm into the caching substrate and completely covers the cache site.
Recovery	Individual places their bill into the caching substrate and retrieves a previously cached item. The bird then eats, re-caches or checks the item (see below).
Looks	Number of looks an individual requires to make its first cache retrieval.
Eat	Individual recovers an item and eats it.
Check	Individual recovers an item and then replaces it immediately into the same cache site.
Re-cache	Individual recovers an item and hides it elsewhere.
Old sites	Individual re-caches a recovered item in a site that previously held a cache.
Same tray	Individual re-caches a recovered item in a previously unused site within the same caching tray.
Other tray	Individual re-caches a recovered item in a previously unused site within the other caching tray.
Out of tray	Individual re-caches a recovered item in a new site in neither of the caching trays, but in some location within the individual's home cage, that will not be removed by the experimenters.

der was pseudorandomised to ensure that no more than two trials of either treatment occurred in succession, with the same observer present during all three observed trials for each storer.

At the end of caching, the food bowl and two caching trays were removed. The number and location of caches made in the trays and in the home-cage were noted, as were the number of worms eaten. Caches made in the home-cage were removed as much as possible.

Ten minutes after the observed trials, the storers were allowed to observe the fate of their caches. One tray was presented to the pilferer for 5 min to retrieve those caches previously made by the storer (subsequently named the 'pilfered tray'). The other tray was placed on a trolley in full-view of the storer and the pilferer, but not accessible to either bird (subsequently named the 'intact tray'). The pilferer's behaviour was recorded during this period including the number of caches recovered, and whether the worms were eaten, re-cached or checked (see Table 1 for a description of behaviours).

Ten minutes after the in-private trials, the two trays were presented on a trolley for 5 min, therefore neither was accessible to either the storer or the pilferer. During this period, the trays were placed equidistant between the storer's and pilferer's cages.

After 4 h, black curtains were erected around the storer's home cage, and the two trays were placed back into the storer's cage, independent of the previous caching treatment. The storer's recovery behaviour [sites visited, caches recovered, and action upon recovery (eaten, re-cached or checked)] was recorded for 5 min, and then the trays were removed. The location of re-caches made by the storer during recovery was also recorded based on four possible re-caching locations; 'old sites', new sites within the 'same tray', 'other tray' or 'outside of the trays' (see Table 1 for definitions).

Statistical analysis

For all analyses, alpha was set at 0.05. For each caching treatment, the mean number of items cached, and the mean number of looks taken to first locate a cache were averaged across the three trials, and the means during observed and in-private trials were compared using Wilcoxon matched-pairs tests (Siegel and Castellan 1988). The mean number of items recovered depends on the number of items available at recovery (AV), which in turn depends on the number cached and whether those caches were subsequently eaten by the pilferer. To take account of this variation in the number of caches available at recovery, we therefore compared the number of caches recovered as a proportion of (1) the number cached in the in-private treatment (C_{T2}), and of (2) the number cached (C_{T1}) minus the number stolen by the pilferer (P_{T1}) in the observed treatment.

The number available at recovery was therefore calculated thus:

$$\mathrm{AV} = C_{T2} + (C_{T1} - P_{T1}) \qquad (1)$$

To compare the recovery behaviour during observed and in-private trials we analysed the proportion of recovered caches that were eaten, re-cached and checked using Wilcoxon matched-pairs tests. For the observed condition we also analysed the location of these re-caches, that is, whether these caches were moved to previously used (old) sites, to new sites within the same tray, to new sites in the other tray or to new sites outside of the trays using Wilcoxon matched-pairs tests. This analysis was not conducted for the in-private condition because re-caching levels were so low. An additional analysis was performed to examine the effects of learning across the three trials within each caching treatment for the number of items cached and the proportion recovered; comparing the proportion eaten, the proportion re-cached and the proportion checked. This analysis was performed using Friedman's ANOVA, with Dunn's multiple comparisons tests for unequal sample sizes used to determine significant differences between trials within each recovery behaviour (Lehner 1996).

Mundry and Fischer (1996) have suggested that inflated *P*-values can result from the use of modern statistical programs to perform non-parametric statistics on low sample sizes. To overcome this difficulty, we performed the Wilcoxon tests using statistical tables (Siegel and Castellan 1988) on those results with a *P*-value close to alpha value for significance ($0.03<P<0.05$). Results with *P*-values in this range are calculated by hand (i.e. without the *Z*-score and exact *P*-values reported). In the one case where the analysis was no longer statistically significant when performed by hand, this result was reported rather than the results from the computer analysis. For the Wilcoxon tests, *n* refers to the number of pairs where a comparison could be made.

Results

Effects of caching treatment

The jays cached significantly more worms when observed by a conspecific than when caching in private, caching a mean of 17.5 and 15 respectively (Wilcoxon pairs test: $T=3$, $n=8$, $P<0.05$). When the pilferers in the observed treatment were presented with one of the storers caching trays, they recovered 52.6% of the caches. However, although pilferers stole caches from the pilfered tray, there were no significant differences between the two treatments in the number of items available at the time of recovery, with a mean of 14.1 in the observed treatment and 15 in the in-private treatment (Wilcoxon: $T=6$, $n=7$, $Z=1.35$, $P=0.18$).

In the observed treatment, jays recovered a mean of 72% of their caches whereas in the in-private treatment they recovered only 48%. This difference between the observed and in-private treatments in the proportion of worms recovered was significant (Wilcoxon: $T=0$, $n=8$, $Z=2.52$. $P=0.01$), but no difference in the number of looks taken to locate the first cache (Wilcoxon: $T=14$, $n=8$, $Z=0.56$, $P=0.58$).

The effects of caching treatment on three different recovery behaviours were analysed separately. There was no significant difference in the proportion of caches eaten (Wilcoxon: $T=12.5$, $n=8$, $Z=0.77$, $P=0.44$), or in the proportion of caches checked (Wilcoxon: $T=10.5$, $n=8$, $Z=1.05$, $P=0.29$), but there were a greater proportion of caches re-cached in the observed treatment compared to the in-private treatment (Wilcoxon: $T=2$, $n=8$, $P<0.05$), with the birds re-caching 15% of their caches in the observed treatment and only 6% of their caches in the in-private treatment.

Effect of pilfered versus intact caching trays

Within the observed treatment, there was no significant difference in the proportion of worms recovered from the pilfered tray versus the intact tray (Wilcoxon: $T=12.5$, $n=7$, $Z=0.25$, $P=0.8$), with the birds recovering a mean of 62% of caches from both trays. More specifically, there were no significant differences between the pilfered tray and the intact tray in the proportion of caches eaten (Wilcoxon: $T=8$, $n=7$, $Z=1.01$, $P=0.31$), in the proportion of caches re-cached (Wilcoxon: $T=5$, $n=7$, $Z=1.52$, $P=0.13$), or in the proportion of caches checked ($T=8$, $n=7$, $Z=0.52$, $P=0.60$).

However, a detailed analysis of re-caching from the pilfered tray during recovery trials in the observed treatment revealed that jays selectively moved the majority of their caches from the pilfered tray to ‘out of tray’ locations in the home cage. Figure 1 shows that the birds re-cached a significantly greater number of worms in out of tray locations than in the same tray (Wilcoxon: $T=0$, $n=7$, $P<0.05$), the other tray (Wilcoxon: $T=0$, $n=7$, $P<0.05$), and old sites (Wilcoxon: $T=0$, $n=7$, $P<0.05$).

In the intact tray (observed treatment), there were no significant differences between the number of items re-cached in out of tray locations compared to locations in the same tray (Wilcoxon: $T=3$, $n=7$, $Z=0.73$, $P=0.47$), the other tray (Wilcoxon: $T=0$, $n=7$, $Z=1.83$, $P=0.07$) or old sites (Wilcoxon: $T=0$, $n=7$, $Z=1.83$, $P=0.07$). However, no re-caches were made in either the other tray or old sites.

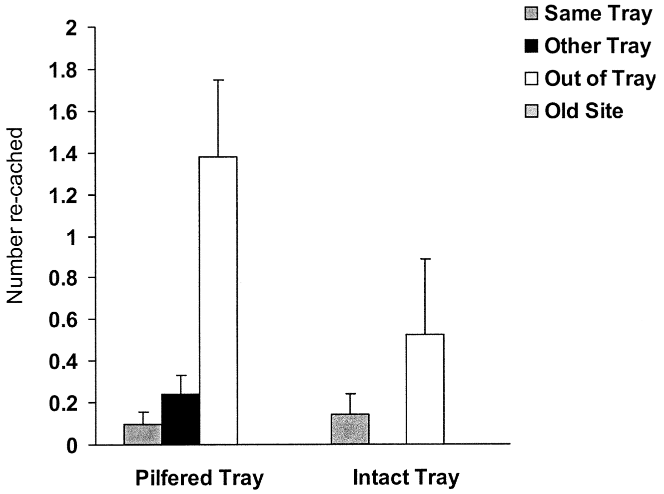

Fig. 1 Mean (±SE) number of re-caches made in different locations: *old sites*, new sites within the *same tray*, new sites within the *other tray* and new sites outside of the two trays (*out of tray*) in the *pilfered* and *intact trays*, during the observed treatment

Therefore, most items that were re-cached from the pilfered tray were made predominantly in sites outside of either caching tray, that is, in places within the bird’s home cage where the caches could be defended and would not be removed by experimenters at the end of the recovery trial. Very few items were re-cached from the intact tray, however those items that were re-cached were placed outside of the trays, with no re-caches made in old sites.

Effect of trial

An analysis of the jays’ recovery behaviour across trials was performed to determine whether the birds had learned to switch strategies after observing their caches being stolen. For example, did the birds compensate for the pilfering by increasing the amount cached once they learned that the observers consistently had the opportunity to subsequently steal their caches? However, there was no effect of trial on the number of worms cached for either the observed treatment (Friedman ANOVA: $\chi^2_2=3.19$, $P=0.20$) or the in-private treatment (Friedman ANOVA: $\chi^2_2=2.84$, $P=0.24$). Within the observed treatment (Fig. 2a), there was a significant effect of trial on the proportion of items eaten (Friedman ANOVA: $\chi^2_2=12.07$, $P=0.002$) and on the proportion of worms checked (Friedman ANOVA: $\chi^2_2=11.47$, $P=0.003$, but not on the proportion of items re-cached (Friedman ANOVA: $\chi^2_2=1.52$, $P=0.47$). Figure 2 shows that these differences arose because the proportion of items eaten increased from trial 1 to trial 2 (Dunn’s test: $Q=3.79$, $k=3$, $P<0.001$). There was no difference between trial 2 and trial 3 (Dunn’s test: $Q=0.5$, $k=3$, $P>0.05$). Conversely, for the proportion of items checked, there was a dramatic decrease from trial 1 to trial 2 (Dunn’s test: $Q=4.16$, $k=3$, $P<0.001$), but no difference between trial 2 and trial 3 (Dunn’s test: $Q=0.56$, $k=3$, $P>0.05$).

Within the in-private treatment there was a significant effect of trial on the proportion of items eaten (Friedman ANOVA: $\chi^2_2=8.44$, $P=0.01$; Fig. 2b). This effect was due to an increase in the proportion of items eaten from trial 1 to trial 3 (Dunn’s test: $Q=2.45$, $k=3$, $P<0.05$). There was no difference between trial 1 and trial 2 (Dunn’s test: $Q=1.91$, $k=3$, $P>0.05$). There was no effect of trial on the proportion of items re-cached (Friedman ANOVA: $\chi^2_2=0.08$, $P=0.67$; Fig. 2b). There was a significant effect of trial on the proportion of items checked (Friedman ANOVA: $\chi^2=6.53$, $P=0.04$; Fig. 2b), however, which decreased from trial 1 to trial 2 (Dunn’s test: $Q=3.20$, $k=3$, $P<0.005$). There was no difference between trial 2 and trial 3 (Dunn’s test: $Q=0.54$, $k=3$, $P>0.05$).

Discussion

The results of this study indicate that when western scrub-jays were observed by a conspecific during caching, and

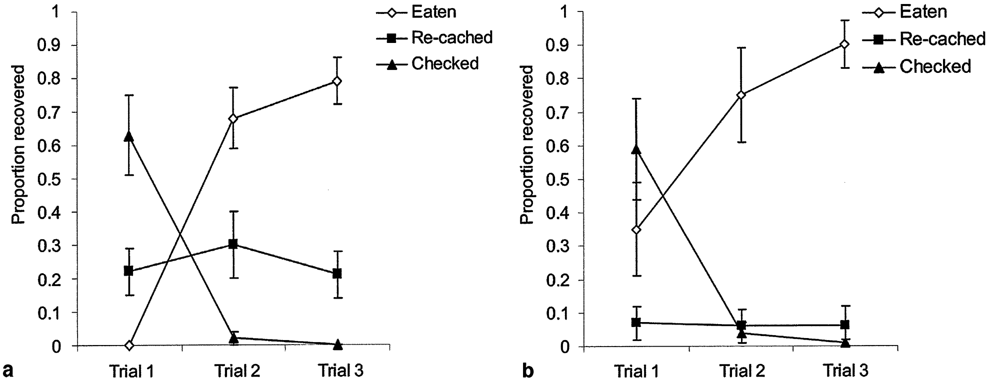

Fig. 2 **a** Mean (±SE) proportion of items recovered and either *eaten*, *re-cached* or *checked* during the observed treatment. **b** Mean (±SE) proportion of items recovered and either *eaten*, *re-cached* or *checked* during the in-private treatment. Proportion recovered was calculated dependent on the number of items that were available at the time of recovery

then they subsequently observed that jay stealing some of their caches from one of two trays, the birds re-cached many of their caches in new sites unavailable to the pilferer (i.e. outside of the caching trays). By contrast, very few items were re-cached (in any location) when the jays had cached in private. This finding extend the results of the Emery and Clayton (2001) study in which birds cached either when observed by a conspecific or in private, but their caches were never stolen (by a conspecific or an experimenter). Furthermore, the more detailed analysis provided by the current study shows that when jays had been observed during caching, they not only re-cached their worms exclusively in new sites that had not been used during caching, but also placed the majority of them in sites outside of both trays in places within the cage where they could be defended, and not pilfered by conspecifics or removed by the human experimenters. Although the birds re-cached significantly more from the trays in which they had been observed caching, there was no statistical difference in the proportion of items re-cached from the pilfered and intact trays. One possibility is that the birds were not attentive to the behaviour of the pilferers and therefore did not discriminate between the two caching trays, but this seems unlikely because the birds avoided searching for caches that the pilferers had already stolen and also avoided re-caching in those sites. In species that rely on an observational spatial memory of where a storer has cached for successful pilfering, one might predict that storers should re-cache from any tray in which they had been watched by a potential pilferer, irrespective of whether the pilferer had been seen to steal the caches. One might argue that in the observed treatment, both the intact and the pilfered trays are potentially at greater risk of cache theft than any trays in which caches have been made in private because of the uncertainty of when the pilferer might have access to the caching trays.

The birds changed their recovery behaviour very quickly after observing a single pilfering event. During recovery the birds could eat their caches, check them and leave them where they were, or re-cache them. Although the proportion of worms that were re-cached did not vary across trials, the proportion eaten and checked changed substantially. On the first trial, the jays checked their caches upon recovery, but ate few. However, once they had experienced an observed trial in which some of their caches had been stolen, they switched to predominantly eating their recovered caches, and dramatically reducing the proportion of caches that were checked. This pattern was identical for the third trial.

As both trays (pilfered and intact) were removed after the recovery period, a sensible strategy to maximise the number of caches that could be utilised during recovery would be to recover as many of the caches as possible, either eating them or re-caching them in sites that are at less risk from pilfering in the future. In the observed condition, the jays appeared to use two such strategies; switch from checking to eating (as checking that caches still remain does not protect them for the future); and re-cache in sites that can be defended from potential pilferers including human experimenters (i.e. sites outside of the caching trays). In the in-private condition, the jays also do not get their caches returned after the recovery period, and they also switch from checking to eating at recovery. Note that the jays in this condition do not demonstrate much overall re-caching and certainly do not display a preference for where they re-cache.

The fact that the scrub-jays changed their responses so quickly suggests that their caching strategies are extremely flexible depending on the social context, which includes whether they are observed during caching (Emery and Clayton 2001), but also whether they see their caches being stolen (present study). Like other food-storing corvids, such as magpies and ravens, jays use a number of different caching and recovery tactics, all of which have the effect of reducing potential pilfering, particularly when foraging in the presence of conspecifics. A number of relatively simple mechanisms may be employed, such as aggressive defence of a larder hoard or territory containing many food stores, or cessation of caching in the presence of potential thieves (e.g. Lahti and Rytkonen 1996, for willow tits). In corvids, however, a number of complex behaviours have been documented, ones that have not been reported for other food-storing species, such as parids. These include delaying caching until the observer has moved away, caching behind a barrier, caching at a distance from potential thieves and varying the density of caches by increasing the spacing between them (Clarkson et al. 1986; Heinrich and Pepper 1998; Bugnyar and

Kotrschal 2002, Robinette Ha et al. 2003). Different strategies are also employed during recovery, such as re-caching food items in new sites when potential thieves are no longer present (Goodwin 1956; Heinrich 1999; Emery and Clayton 2001).

These observations suggest that food-caching corvids may differ from other food-storing species such as parids in the complexity of the strategies used to minimise cache theft. Indeed, the scrub-jays' behaviour is consistent with a more complex interpretation because they act during recovery in a manner that would significantly reduce the potential for future pilfering by re-caching and the tactics used depend on the context. The extent to which this behaviour is unique to corvids remains an open question because there is only one published study of a non-corvid. Stone and Baker (1989) stated that "the possibility exists that false caches and re-caches are strategies for protecting caches from theft by another bird if the thief could learn the location of caches by observing the cacher" (Stone and Baker 1989, p 887). However, in their test of the effects of conspecifics on caching behaviour in black-capped chickadees, they found a reduction in caching intensity, but no evidence of re-caching or false caching. The present finding that corvids may use sophisticated cognitive tactics in their prevention of pilfering is not entirely surprising given that corvids have also demonstrated other flexible cognitive abilities, such as episodic-like memory (Clayton and Dickinson 1998; Clayton et al. 2001a), insight (Heinrich 2000), and tool construction and manipulation (Hunt 1996; Weir et al. 2002), similar to those demonstrated by monkeys and apes (Emery and Clayton 2003). Future experiments will focus on which cues control the specific re-caching outside of the caching trays during recovery and whether it depends on who is watching and stealing. Stellar's jays (*Cyanocitta stelleri*), for example, steal Grey jays' (*Perisoreus canadensis*) caches, whereas Clark's Nutcrackers (*Nucifraga columbiana*) do not. In a laboratory experiment, Grey jays were observed either by a conspecific, a Clark's Nutcracker or a Stellar's jay. The Grey jays cached as usual in front of the conspecific and the Clark's Nutcracker, but did not cache in front of the Stellar's jays (Burnell and Tomback 1985). Additional cues to potential theft may be the attentional state (i.e. are they preoccupied?), or motivational state (i.e. are they hungry or satiated?) of conspecifics and whether there is a relationship between the storer and observer, such as kin or social partners. Such studies should provide a tractable method for testing complex social cognition.

Acknowledgements This work was supported by grants to N.S.C. from the National Institutes of Health NS 35465-05 and MH2602, BBSRC grant S16565 and the University of Cambridge. N.J.E. was funded by a Medical Research Council programme grant to E.B. Keverne, and by a Royal Society University Research Fellowship. We thank Sabine Tebbich for comments on an earlier version of the manuscript. These experiments comply with the UK Home Office regulations concerning animal research and welfare, as well as University of Cambridge regulations on the use of animals.

References

Baker MC, Anderson P (1995) Once-pilfered cache sites not avoided by black-capped chickadees. Anim Behav 49:1599–1602

Balda RP, Kamil AC (1989) A comparative study of cache recovery by three corvid species. Anim Behav 38:486–495

Balda RP, Kamil AC (1992) Long-term spatial memory in Clark's nutcrackers, *Nucifraga columbiana*. Anim Behav 44:761–769

Bednekoff PA, Balda RP (1996a) Social caching and observational spatial memory in pinyon jays. Behaviour 133:807–826

Bednekoff PA, Balda RP (1996b) Observational spatial memory in Clark's nutcrackers and Mexican jays. Anim Behav 52:833–839

Brockmann HJ, Barnard CJ (1979) Kleptoparasitism in birds. Anim Behav 27:487–514

Bugnyar T, Kotrschal K (2002) Observational learning and the raiding of food caches in ravens, *Corus corvax*: Is it "tactical" deception? Anim Behav 64:185–195

Burnell KL, Tomback DF (1985) Stellar's jays steal gray jay caches: field and laboratory observations. Auk 102:417–419

Clarkson K, Eden SF, Sutherland WJ, Houston AI (1986) Density dependence and magpie food hoarding. J Anim Ecol 55:111–121

Clayton NS, Dickinson A (1998) Episodic-like memory during cache recovery by scrub jays. Nature 395:272–274

Clayton NS, Dickinson A (1999) Scrub jays (*Aphelocoma coerulescens*) remember the relative time of caching as well as the location and content of their caches. J Comp Psychol 113: 403–416

Clayton NS, Griffiths DP, Emery NJ, Dickinson A (2001a) Episodic-like memory in animals. Philos Trans R Soc Lond B 356:1483–1491

Clayton NS, Yu K, Dickinson A (2001b) Scrub jays (*Aphelocoma coerulescens*) can form integrated memory for multiple features of caching episodes. J Exp Psychol Anim Behav Proc 27:17–29

DeGange AR, Fitzpatrick JW, Layne JN, Woolfenden GE (1989) Acorn harvesting by Florida scrub-jays. Ecology 70:348–56

Emery NJ, Clayton NS (2001) Effects of experience and social context on prospective caching strategies by scrub jays. Nature 414:443–446

Emery NJ, Clayton NS (2003) Comparing the complex cognition of birds and primates. In: Rogers LJ, Kaplan G (eds) Comparative vertebrate cognition: are primates superior to non-primates? Kluwer, Amsterdam, in press

Goodwin D (1956) Further observations on the behaviour of the jay. Ibis 98:186–219

Hampton RR, Sherry DF (1994) The effects of cache loss on choice of cache sites in black-capped chickadees. Behav Ecol 5:44–50

Heinrich B (1999) Mind of the raven. Harper, New York

Heinrich B (2000) Testing insight in ravens. In: Heyes CM, Huber L (eds) The evolution of cognition. MIT Press, Cambridge, Mass., pp 289–309

Heinrich B, Pepper J (1998) Influence of competitors on caching behaviour in common ravens, *Corvus corax*. Anim Behav 56: 1083–1090

Hitchcock CL, Sherry DF (1995) Cache pilfering and its prevention in pairs of black-capped chickadees. J Avian Biol 26: 181–192

Hunt GR (1996) Manufacture and use of hook-tools by New Caledonian crows. Nature 379:249–251

James PC, Verbeek NAM (1983) The food storage behaviour of the northwestern crow. Behaviour 85:276–291

Kallander H (1978) Food hoarding in the rook, *Corvus frugilegus*. Anser Suppl 3:124–128

Krebs JR, Davies NB (1993) An introduction to behavioural ecology, 3rd edn. Blackwell, Oxford

Lahti K, Rytkonen S (1996) Presence of conspecifics, time of day, and age affect willow tit food hoarding. Anim Behav 52:631–636

Lehner, PN (1996) Handbook of ethological methods, 2nd edn. Cambridge University Press, Cambridge

Mundry R, Fischer J (1996) Use of statistical programs for nonparametric tests of small samples often lead to incorrect *P*-values: examples from Animal Behaviour. Anim Behav 58:256–259

Preston SD, Jacobs LF (2001) Conspecific pilferage, but not presence affects Merriam's kangaroo rat cache strategy. Behav Ecol 12:517–523

Robinette Ha R, Bentzen P, Marsh J, Ha JC (2003) Kinship and association in social foraging Northwestern crows (*Corvus caurinus*). Bird Behav 15:65–75

Siegel S, Castellan NJ Jr (1988) Nonparametric statistics for the behavioural sciences. McGraw-Hill, New York

Stone ER, Baker MC (1989) The effects of conspecifics on food caching by black-capped chickadees. Condor 91:886–890

Vander Wall SB (1990) Food hoarding in animals. University of Chicago Press, Chicago

Ward PS, Zahavi A (1973) The importance of certain assemblages of birds as 'information centres' for food finding. Ibis 115: 517–534

Weir AAS, Chappell J, Kacelnik A (2002) Shaping of hooks in New Caledonian crows. Science 297:981