

Mountain chickadees discriminate between potential cache pilferers and non-pilferers

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Evolution of complex cognition in animals has been linked to complex social behaviour. One of the costs of sociality is increased competition for food which may be reduced by food caching, but cache theft may undermine the benefits of caching. In birds, sophisticated food-caching-related cognition has been demonstrated only for corvids and attributed to their highly social behaviour. Many non-corvid food-caching species exhibit similar complex social behaviour and here I provide experimental evidence that mountain chickadees (*Poecile gambeli*) adjust their caching strategies depending on social context. Chickadees were allowed to cache seeds in the presence of potential cache pilferer, either conspecific or heterospecific (red-breasted nuthatch, *Sitta canadensis*) and a non-pilferer (dark-eyed junco, *Junco hyemalis*) positioned at the opposite sides of the experimental arena. Available caching sites were either exposed to these observers or hidden from their view while the cacher could always see both observers. Chickadees chose caching sites that were hidden from direct view of the potential pilferers while caching in direct view of the non-pilferers. When no pilferers were present, chickadees made equal use of all available caching substrates and there were no differences in the amount of caching in the presence or absence of pilferers. These results suggest that (i) chickadees may be able to recognize potential cache thieves, both conspecific and heterospecific, and adjust their caching strategies to minimize potential cache pilferage and (ii) chickadees appear to discriminate between caching sites that can or cannot be seen by observers, which may allow them to control visual information available to potential pilferers.

Keywords: food caching; avian cognition; cache protection; chickadee; cognition

1. INTRODUCTION

Among animals, primates have been traditionally considered most intelligent while birds have often been thought of as ‘bird brains’ or animals whose behaviour is controlled mostly by instincts (Emery & Clayton 2004, 2005). Recent research with birds, however, suggests that such a view is overly simplistic as some bird species appear to show fairly complex cognition, similar to that in primates (Emery & Clayton 2004, 2005; Raby *et al.* 2007). Among birds, it has been suggested that the corvids are capable of the most flexible and complex cognition and such advanced cognitive abilities have been linked to their complex social behaviour (Emery & Clayton 2004). Emery & Clayton (2004) even argued that corvids and apes share similar levels of cognition which could be a result of convergent evolution triggered by similar socio-ecological environment.

Most research on cognition in corvids focused on food-caching species because food-caching behaviour provides an excellent paradigm to investigate cognition. Corvids have been shown to have complex food-caching-related cognition. Food-caching behaviour has probably evolved in response to unpredictable environments in which storing surplus food for later consumption could have a strong impact on survival. Food caching may also be beneficial in social species by reducing competition for naturally available food, but to gain the most benefits the cacher should be able to successfully retrieve its own food caches. Most food-caching birds are indeed well

known for memory use in cache retrieval (Emery & Clayton 2004). In addition to excellent spatial memory, some food-caching corvids have been shown to use episodic-like memory by remembering location, timing and content of all food caches (Clayton & Dickinson 1998).

Relocating caches, however, is only one aspect of successful food caching because if these caches were pilfered they would be of no benefit to the storer. Thus, there might be a high selection pressure on behavioural cache management that would minimize cache loss due to pilferage (Emery & Clayton 2001; Emery *et al.* 2004; Dally *et al.* 2006a,b). Corvids, most notably western scrub-jays (*Aphelocoma californica*) and ravens (*Corvus corax*), have been shown to have complex and flexible cognitive skills related to cache protection; they appear to recognize specific individuals that observed them during caching events, seem to base their response to being observed on their own previous experience of stealing caches and also seem to mislead their conspecifics when making caches (Emery & Clayton 2001; Bugnyar & Kotrschal 2002, 2004; Emery *et al.* 2004; Bugnyar & Heinrich 2005; Dally *et al.* 2006a,b). Western scrub-jays also appear to be capable of recognizing what the observers can and cannot see and adjust their caching behaviour to prevent the transfer of visual information to potential cache thieves (Dally *et al.* 2004). Demonstration of such complex food-caching-related cognitive skills in corvids led Emery *et al.* (2004) to conclude that corvids may significantly differ from other food-caching birds, such as parids.

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However, non-corvid food-caching species, such as chickadees (parids), also exhibit highly social behaviour. In many aspects, socioecological environment of food-caching parids may be even more complex than that in many corvid species. For example, most food-caching parids spend the non-breeding season in social groups with stable membership and strict dominance hierarchy (Hogstad 1989). Territories of such social groups border and/or slightly overlap territories of neighbouring groups and most parids also regularly join mixed-species flocks (Hogstad 1989; Harrap & Quinn 1995). While joining such complex social groups has benefits, the costs might include increased competition for food and increased risk of cache pilferage. Field data clearly show that cache pilferage does occur in populations of food-caching parids (Brodin 1993). In such conditions, the selection pressure for mechanisms of cache theft prevention should be especially high.

Previous work with food-caching parids suggested that they may be sensitive to the risk of pilferage (Stone & Baker 1989; Hampton & Sherry 1994; Lahti *et al.* 1998). Observational memory has been well documented in food-caching corvids (Bednekoff & Balda 1996a,b) and, based on similar socioecological environment, it might be expected in food-caching parids as well. However, attempts to establish whether chickadees can use observational memory to steal caches have failed (Baker *et al.* 1988, 1990; Baker & Anderson 1995; Hitchcock & Sherry 1995). Previous studies mainly focused on the cognitive abilities of the observer–potential pilferer. However, it may be difficult to ensure that a wild-caught chickadee placed in a small cage would pay attention to the environment outside the cage, thereby reducing the likelihood of documenting observational memory. By focusing instead on the cacher, it may be possible to gain additional insights into the food-caching-related strategies (Clayton *et al.* 2007).

Here, I used mountain chickadees (*Poecile gambeli*) to investigate whether and how caching decisions may be affected by social context and potential risk of pilferage. In my study area, mountain chickadees often coexist with several other species, most notably the red-breasted nuthatch (*Sitta canadensis*) and the dark-eyed junco (*Junco hyemalis*) (V. V. Pravosudo 1999–2007, personal observations). Juncos do not cache food (Nolan *et al.* 2002) and also do not pilfer caches made by chickadees and nuthatches (V. V. Pravosudo 1999–2007, personal observations). Because dark-eyed juncos forage mostly on the ground (Nolan *et al.* 2002) and chickadees and nuthatches forage and store food only in trees above the ground (V. V. Pravosudo 1999–2007, personal observations), juncos simply could not pilfer their caches (Nolan *et al.* 2002). Both the mountain chickadees and the red-breasted nuthatches cache food and are likely to pilfer each other's caches. Even though chickadees and nuthatches use different foraging niches, nuthatches forage mostly on tree trunks while chickadees forage mostly among the tree branches and twigs (Ghalambor & Martin 1999; McCallum *et al.* 1999), both species eat and store pine seeds which they extract from pine cones. Red-breasted nuthatches are smaller than mountain chickadees (9.8 g, Ghalambor & Martin 1999, versus 12.0 g, V. V. Pravosudo 1999–2005, unpublished data, $n=75$), but their dominance relationship is unclear. It appears that in natural conditions both species might coexist without much interspecific

aggression (Kilham 1975; V. V. Pravosudo 1999–2007, personal observations). In my study site in Tahoe National Forest, California, I have also not seen aggression between these two species when they were intensely caching both pine seeds from cones and sunflower seeds from feeders in late summer–autumn.

The goal of this study was to test whether chickadees choose cache sites that would minimize risk of pilferage, which would suggest that they may be able to discriminate between potential pilferers, both conspecific and hetero-specific, and heterospecific non-pilferers. Because chickadees and nuthatches often forage and store food within close proximity to one another, and thus within each other's field of vision, another prediction in this study was that chickadees should minimize the amount of visual information available to potential pilferers by specifically choosing cache sites that cannot be seen only by the pilferers. Alternatively, it may be predicted that chickadees might also increase the distance of caches from potential pilferers or cache in sites from which chickadees themselves could not see potential pilferers ('out-of-sight, out-of-mind'; Clayton *et al.* 2007). All of these strategies should reduce the risk of cache pilferage. At the same time, chickadees should ignore non-pilferers when making caching decisions.

2. MATERIAL AND METHODS

Twelve mountain chickadees, six red-breasted nuthatches and six dark-eyed juncos were captured with mistnets around Sagehen creek in Tahoe National Forest (California) during November 2006. All birds were transported to the University of Nevada Reno and placed singly in wire-mesh cages (44 × 61 × 61 cm). Birds were maintained on 9 L : 15 D winter photoperiod throughout the entire experiment and provided water and food ad libitum (chickadees and nuthatches: pine nuts, sunflower seeds and mealworms; juncos: a seed mix and mealworms). After a three-week adjustment to captivity, chickadees were familiarized with the experimental room (218 × 373 × 263 cm); each bird spent three 2 h periods separated by 2 days in the experimental area. Pine nuts were available in two feeders as well as in some of the caching sites to stimulate caching behaviour. All holding cages were connected to the experimental room by openings through a wall separating holding and experimental rooms (Pravosudov & Clayton 2001, 2002). The process of letting a bird into the experimental room involved opening the cage door and the opening cover on the wall, and turning the lights off in the holding room, which stimulated the bird to fly into the experimental room with lights on. When the bird flew into the experimental room, the cage door connected to the wall opening was closed until the bird was required to go back into the holding cage. At that time, the lights were reversed and the bird flew back into its holding cage (Pravosudov & Clayton 2001, 2002). This procedure allowed moving birds without handling them. The experimental room contained two caching 'trees' made of square wooden posts (8.5 × 8.5 cm) extending from the floor to the ceiling. These caching posts were positioned 96 cm from the walls along the long side of the room and in the middle between the walls along the short side (figure 1). Each post had 20 caching holes (6 mm in diameter, 5 mm deep), 10 on each of the two opposite sides with no holes on the other two sides of the square posts (figure 1). The two lowest caching holes were

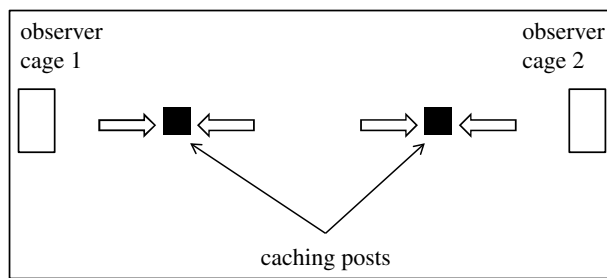


Figure 1. Experimental room set-up. Thick arrows indicate four available caching surfaces (10 caching sites in each surface) in 4×4 caching posts.

46 cm above the floor and the holes above were located every 20 cm. A wooden perch (1 cm in diameter) was positioned below each caching hole in the middle of the post.

After all birds were familiarized with the experimental set-up, each individual chickadee was allowed to cache in the experimental room in three different conditions. All 12 mountain chickadees were tested individually every third day for five trials during each of the three experimental conditions. During each trial, each bird was allowed to cache seeds for 30 min in the experimental room. To stimulate caching, all birds were deprived of food 2 hours before the lights were turned off in the evening before testing day. Testing started 1 hour after lights were turned on in the morning and birds did not have any food prior to testing. Four birds were tested each day and the order of birds for testing was reversed between the trials to assure a similar level of food deprivation. Two feeders full of pine nuts were available at two opposite sides of the room. Birds were observed through a one-way glass and all food-caching activities were recorded. After birds were removed from the experimental room, the location of all caches was verified and all caches were removed. Previous studies on chickadees suggested that removing caches should not result in reduced caching rates in consequent trials (Lucas *et al.* 2001). Experiments lasted from 2 January to 12 March 2007.

In all experimental conditions, two cages ($25 \times 47 \times 31$ cm) were positioned at two opposite sides of the room (along the long side; figure 1). Cages were elevated above the floor level so that the bottom of the cage was 47 cm above the floor. The front side of the cages was 61 cm from the nearest caching post; two caching surfaces (one on each post) were directly facing the cages and the other two were on the opposite sides of the square caching posts (figure 1). Under the first experimental condition, one cage contained a mountain chickadee while the other contained a dark-eyed junco. Under the second experimental condition, one cage contained a red-breasted nuthatch while the other contained a dark-eyed junco. The third condition was a control treatment in which both cages were empty. In the first two conditions, the position of each observer was determined randomly and then alternated during each trial so that each experimental bird had the opportunity to cache with a chickadee or a nuthatch as the observer at both sides of the room. Individual observers of all three species were alternated between each trial so that all caching chickadee experienced different individual observers during different trials. All trials with the red-breasted nuthatch as the observer followed the trials with the mountain chickadee as the observer. Control trials with no observers were randomly distributed within the trials in both experimental conditions.

For the analyses, the caching surface numbering always started from the surface directly facing a chickadee or a nuthatch observer. The surface facing a chickadee or a nuthatch observer was always designated as 'surface 1', the surface on the opposite side of the same post was 'surface 2', the surface on the second post facing the side of the room with a chickadee/nuthatch observer was 'surface 3' and the opposite surface on the second post (always facing a dark-eyed junco observer) was 'surface 4'. Because the position of the chickadee/nuthatch observer was alternated between each trial, such numbering was relative to the position of the observer-pilferer. The chickadee/nuthatch observers had a clear view of the first caching surface while they could not see any caching sites on the second and fourth surfaces and the view of the third surface was severely obscured by the caching post in front of it (figure 1). The junco observer, on the other hand, had a clear view of the fourth surface while they could not see any caching sites on the third and first surfaces and the view of the second surface was obscured by the caching post. Alternating the position of chickadee/nuthatch and junco observers between the opposite sides of the room avoided potential biases in caching locations relative to the room topography.

A caching bird had a good view of both observers from any caching location because the square caching posts were only 8.5 cm thick, and so the bird sitting on a perch in the middle (4.25 cm from either edge) can easily see what is behind the post. Chickadees always sat on a perch parallel to the caching surface of the post, so the head of the bird extended slightly beyond the edge of the post (chickadee length is approx. 10–12 cm) allowing a view of the observer behind the post. Only when a chickadee was actually placing a seed into a caching hole, its head faced a caching surface and at that particular moment the chickadee could not see the observer. Observers also were able to see a chickadee cacher at all locations, but they had a full view of the entire body of the bird cacher only when the cacher was sitting on a perch located on the surface directly facing the observer (surface 1). When the cacher was sitting on perches located on the other three caching surfaces, the observer could only see small areas of the cacher's body (part of the head and/or tail) that may be protruding beyond the caching post. Also, when the cacher was actually placing a seed into a caching hole located on surfaces 2–4, it was mostly out of the observers' view because at that brief moment, the cacher positioned its body perpendicular to the caching surface. Irrespective of the observer position within its small cage, caching sites on surfaces 2–4 could not be well seen by the observer.

For statistical analyses, the total number of caches made during all five trials for each experimental condition was used. To test whether there were significant differences in the number of caches made on four available caching surfaces, a repeated measures ANOVA was employed with caching surface as a repeated factor. Tukey's *post hoc* tests were used to test for specific differences between the four available surfaces.

3. RESULTS

There were no significant differences in the total number of food caches between the two experimental conditions (chickadee–junco or nuthatch–junco observers) and control trials with no observers (repeated measures ANOVA, $F_{2,22} = 0.95$, $p = 0.40$). Chickadees used the feeder next to

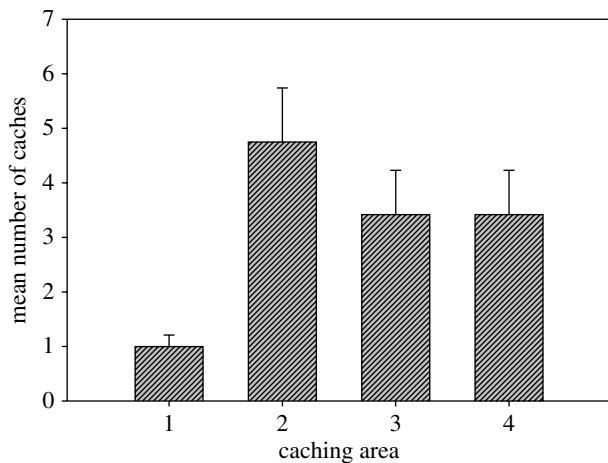


Figure 2. Mean number of caches made by mountain chickadees on four available caching surfaces during five trials with another mountain chickadee and a dark-eyed junco as observers. Surface 1 always faced a chickadee observer and surface 4 faced a dark-eyed junco observer. Caching sites in surfaces 2, 3 and 4 could not be easily observed by the chickadee observer owing to their position relative to the observer.

the pilferer/observer more frequently than the feeder next to the non-pilferer junco ($F_{1,11}=7.53$, $p=0.02$).

There were significant differences in the number of caches made by chickadees on four available caching surfaces in the presence of another mountain chickadee and a dark-eyed junco (repeated measures ANOVA, $F_{3,33}=7.56$, $p<0.001$). Tukey's *post hoc* analysis revealed that chickadees cached significantly fewer seeds on the surface facing the observer chickadee (surface 1) compared with the other three surfaces (surfaces 2, 3, 4; $p<0.05$; figure 2). There were no significant differences in the amount of cached seeds between the other three caching surfaces, including the surface facing the dark-eyed junco ($p>0.1$; figure 2).

When a red-breasted nuthatch and a dark-eyed junco were present as observers, there were also significant differences in the number of cached seeds between the four available caching surfaces (repeated measures ANOVA, $F_{3,33}=6.96$, $p<0.001$). *Post hoc* analyses indicated that chickadees made significantly fewer caches on the surface facing the red-breasted nuthatch (surface 1) compared with the other three surfaces (surfaces 2, 3, 4; figure 3; $p<0.05$) while there were no significant differences in the number of caches between these three surfaces, including the surface facing the dark-eyed junco ($p>0.1$; figure 3).

When no bird observers were present in the experimental room, there were no significant differences in the number of cached seeds between all four available caching surfaces (repeated measures ANOVA, $F_{3,33}=0.30$, $p=0.82$; figure 4).

When the total number of caches made only on the first caching surface always facing the observer/pilferer was compared between the three experimental conditions, there were significant differences between these conditions ($F_{2,22}=13.34$, $p<0.001$). Tukey's *post hoc* analyses revealed that there were no differences in the number of caches on the first surface between the chickadee/observer and the nuthatch/observer conditions ($p=0.58$), but both of these conditions were significantly different from the control condition when no observers were present ($p<0.01$).

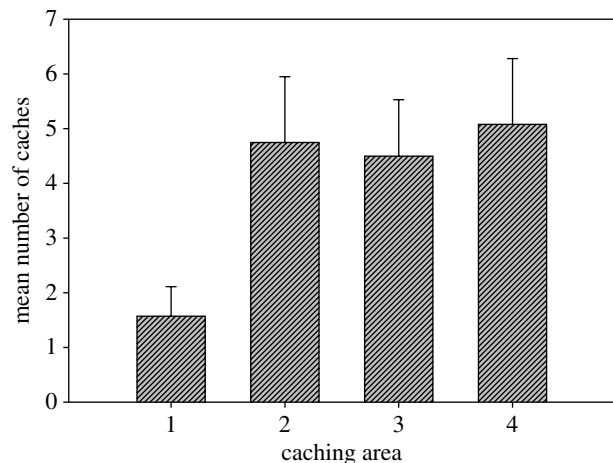


Figure 3. Mean number of caches made by mountain chickadees on four available caching surfaces during five trials with a red-breasted nuthatch and a dark-eyed junco as observers. Surface 1 always faced a red-breasted nuthatch and surface 4 faced a dark-eyed junco. Caching sites in surfaces 2, 3 and 4 could not be easily observed by the nuthatch observer owing to their position relative to the observer.

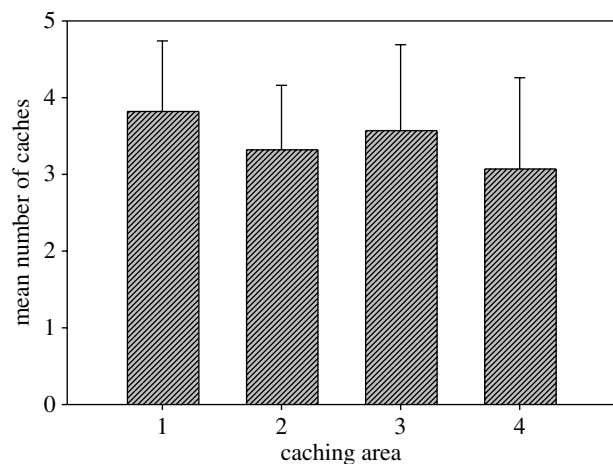


Figure 4. Mean number of caches made by mountain chickadees on four available caching surfaces during five control trials with no observers present.

4. DISCUSSION

The experiment demonstrated that mountain chickadees avoided using caching sites which were in direct view of either another mountain chickadee or a red-breasted nuthatch and instead used caching sites which could not be observed by these species. In contrast, chickadees freely used caching sites in direct view of dark-eyed juncos. Because the location of the chickadee/nuthatch and junco observers were alternated between each trial, these results suggest that chickadee choices of caching sites were influenced by the species of the observer and not by their potential preferences for specific cache sites or locations within the room. When no observers were present, chickadees used all four caching surfaces equally. These findings suggest that chickadees were hiding their caches from the view of potential cache pilferers (other chickadees and red-breasted nuthatches) but not from that of non-pilferers (dark-eyed juncos) and, therefore, it appears that mountain chickadees might have evolved the ability to recognize potential thieves of their caches, including thieves of different species.

Chickadees did not reduce the amount of caching in the presence of potential pilferers which suggests that their caching behaviour was not suppressed by perceived threat of aggression from either conspecific or heterospecific observers. These results differ markedly from an observation by Burnell & Tomback (1985) showing that gray jays (*Perisoreus canadensis*) completely stopped caching in the presence of Steller's jays (*Cyanocitta stelleri*). It is not clear, however, whether gray jays specifically responded to the risk of cache theft or to the perceived threat of aggression from a dominant species. If Steller's jays were socially dominant to gray jays, gray jays may have suppressed all activity irrespective of whether they recognized that Steller's jays may pilfer their caches or not. Subordinate western scrub-jays also suppress their caching in the presence of dominants (Dally *et al.* 2005a,b). Unlike the Burnell & Tomback (1985) study, Dally *et al.* (2004, 2005a,b, 2006a) studies demonstrated that western scrub-jays seem to recognize the identity of potential conspecific cache pilferers and store food either away from them or in sites that cannot be easily observed. On the other hand, there seem to be no experimental data showing that corvids recognize and respond similarly to heterospecific cache thieves. This study provides the first experimental data for a non-corvid species, which suggest that mountain chickadees may discriminate between and respond to potential cache thieves and non-thieves, both conspecific and heterospecific, by storing food in sites that could not be easily observed by these thieves.

Mountain chickadees also did not seem to cache farther away from the potential pilferer. If chickadees were trying to move caches as far away as possible from potential pilferers they would have cached significantly less in both surfaces on the caching post closest to the pilferer compared with the two available surfaces on the second post which was further away. Instead, chickadees used the second surface as often as they used the other two surfaces which were further away. Chickadees were also able to see the pilferers from either of the two caching posts and so caching on the second post, which was slightly further away from the pilferer, was effectively caching in sites that cannot be easily seen by the observer/pilferer rather than moving caches so far that the pilferer would be out of sight of the cacher.

It is possible that chickadees used caching posts as a physical barrier against potential threat from pilferers because caching chickadees might have perceived the caching surface opposite to the pilferer as safer from immediate threat of aggression. For a chickadee, both other mountain chickadees and red-breasted nuthatches, but not dark-eyed juncos, are possible competitors for food. Mountain chickadees are larger than red-breasted nuthatches but no aggressive interactions have been reported for these species during food-caching periods and, therefore, caching food out of view of nuthatch observers might not have been necessarily caused by potential threat of immediate aggression. On the other hand, nuthatches might still be able to steal caches soon after chickadees made them because chickadees do not seem to protect their caches and thus caching on the surfaces not easily observable by potential pilferers might provide better chances against immediate pilferage.

The same is true for chickadee observers because only if the observer was a dominant might the subordinate

cacher have perceived potential aggressive threat. Even though dominance status of chickadees in the experiment was not known, each of the 12 cachers experienced different chickadee observers at different trials and thus it is likely that some observers were dominant while others were subordinate to the cacher. If a cacher was dominant to an observer, it should perceive no aggressive threat from the observer and its caching decisions should not be affected by the observer. The results, however, showed that all cachers stored food in sites not visible to the chickadee observer, suggesting that these decisions were not probably influenced by potential perceived threat of immediate aggression from chickadee observers.

Finally, if cachers would have perceived threats of immediate aggression from observers-pilferers (either nuthatches or chickadees), they would have probably stopped caching altogether as was the case in studies of gray jays and Steller's jays (Burnell & Tomback 1985) and dominant and subordinate scrub-jays (Dally *et al.* 2005a,b). The chickadees, however, cached as much with either a chickadee or a nuthatch observer as they did without any observers. It is also not clear whether chickadees or nuthatches can successfully and aggressively pilfer caches at the moment another chickadee is making rather than stealing them after the cacher has left. Lahti *et al.* (1998) described several unsuccessful attempts by dominant willow tits (*Parus montanus*) to aggressively pilfer caches from subordinates at the moment of caching, but in each case the subordinate flew away with the cache. On the other hand, Lahti *et al.* (1998) also described pilfering by both dominants and subordinates after the cacher left the location. There is also evidence that caches in parids may be pilfered days or weeks after they were made (Brodin 1993).

Caching chickadees could see the observer birds from all caching locations while the observer could not see the caching locations on the surfaces facing away and the surface behind the post closest to the observer. Previous studies with food-caching corvids showed that cachers prefer to hide food behind the divider separating the cacher and the observer (review in Clayton *et al.* (2007)). One potential explanation of this behaviour might be that cachers respond to their own visual information and cache in areas in which they cannot see the observers ('out-of-sight, out-of-mind' hypothesis; Clayton *et al.* 2007). Further experiments with scrub-jays, however, suggested that this hypothesis is not likely because scrub-jays also cached in hard-to-see sites when no dividers were present (Dally *et al.* 2004; Clayton *et al.* 2007). The 'out-of-sight, out-of-mind hypothesis' also is not likely to explain the results presented here because potential pilferers were always within a view of the caching chickadee (Dally *et al.* 2004; Clayton *et al.* 2007). Instead, this experiment suggests that chickadees might be able to perceive the information about visual range of the observers, rather than rely on their own visual range, and use this information in their caching decisions in order to minimize the risk of cache theft.

During the precise moment of caching with its beak directly against the caching surface, caching chickadees could not see the observer-pilferer for a very brief period of time and so it remains possible that chickadees did use caching posts as a physical barrier which might be consistent with the out-of-sight, out-of-mind hypothesis.

However, under extremely short duration of actual caching (less than a second), it is unlikely that a chickadee would place an observer 'out of mind' given the fact that the observer was easily seen immediately prior and after the caching event. If chickadees caching was based on the out-of-sight, out-of-mind hypothesis because they could not see the observer–pilferer for a brief time period of actual caching, then it may be expected that chickadees would have also used the surface in direct view of the observers–pilferers, in which case the cashers would also not have the observer in their direct view (as they would be sitting with their back towards the observer and with their beak towards the caching surface away from the observer). In this experiment, however, chickadees chose not to use the surface in direct view of pilferer–observer. Nevertheless, the out-of-sight, out-of-mind hypothesis cannot be completely ruled out because for a brief moment of actual caching chickadees did not see the observer–pilferer.

It is possible that chickadees' caching decisions were affected by observers' behaviour rather than by what the observers can or cannot see and chickadees may have simply been avoiding threat from the observers (both chickadees and nuthatches) and ignoring juncos as a consequence, rather than treating juncos as a non-threat. However, in this case chickadees should be caching mostly on surfaces 3 and 4 (furthest possible from potential threat) and less on surface 2 which is closer to potential threat. Instead, chickadees used all three surfaces equally and avoided only the surface in direct view of the observers–pilferers. The fact that chickadees used the fourth surface exposed to junco observers as much as they used the other two surfaces suggests that chickadees did not perceive juncos as a potential threat to their caches. Experimental design also prevented birds from escaping the observers' view and so the available options were either to cease caching altogether if birds perceived a threat from aggressive observers or to cache in sites that are not in direct view of the observer–pilferer. The fact that the chickadees did the latter suggests that their behaviour was more likely influenced by their discrimination between what the observer can or cannot see rather than by observers' behaviour.

Birds used in this study were wild caught with unknown previous experiences and it is possible that they may have learned from past experiences that caching in direct view of other chickadees and nuthatches may result in cache loss (Emery & Clayton 2001). Hampton & Sherry (1994) showed that chickadees avoid reusing caching sites from which caches were pilfered suggesting that chickadees can learn the association of potential sites with risk of pilferage. Learning the association between specific observer species and caching sites that were in direct view of these species during caching events, however, appears much more complex than learning that a specific site is always prone to pilferage.

Previous experiments failed to demonstrate that chickadees can use observational memory to pilfer caches (Baker *et al.* 1988, 1990; Hitchcock & Sherry 1995), but nevertheless it remains hypothetically possible that chickadees may still use it. One argument against chickadees using observational memory might be the fact that cashers were always visible to the observers. It may potentially be predicted that simply seeing a cacher might provide the salient cues to the observers to

remember cacher's locations to be pilfered later (Clayton *et al.* 2007). However, chickadees live in fairly large multispecies flocks with most flock members being a cacher and an observer at the same time and very often within each others' view. In such systems, simply following the cacher might be highly inefficient because every bird is also involved in many other non-caching activities, whereas observing and remembering actual caching events and locations of caches might be the most efficient method of pilfering. Pinyon jays (*Gymnorhinus cyanocephalus*), for example, cache food in tight large flocks in which most birds are probably within the view of each other, yet it is well known that pinyon jays can use observational memory to locate each other's caches (Bednekoff & Balda 1996a).

Alternatively, chickadees may be caching outside of the pilferers' view simply to avoid immediate cache theft which does not require observational memory. Either way, it remains unclear whether chickadees are even capable of using observational memory to steal other chickadees' caches, and further experiments investigating observational memory in chickadees are necessary.

Overall, results of this experiment suggest that mountain chickadees may be able to discriminate between potential cache pilferers, both conspecific and heterospecific, and heterospecific non-pilferers. It also appears that chickadees may be able to discriminate between the sites that an observer can or cannot see and they may be specifically choosing caching sites that cannot be seen by potential pilferers. This is, to my knowledge, the first demonstration of such social context-dependent food-caching behaviour in a non-corvid avian species, and it does not seem to agree with the suggestion that food-caching parids may be fundamentally different from food-caching corvids in the complexity of behavioural strategies used to prevent cache theft (Emery *et al.* 2004; Clayton *et al.* 2007).

It remains possible, however, that chickadee behaviour is much simpler than that of corvids and that chickadees used caching posts as physical barriers against potential pilferers which would reduce the chances of immediate theft. It also remains possible that in the wild, chickadees might use a variety of cache pilferage prevention behaviours including caching at a larger distance from potential pilferers and using caching locations from which the observer is not visible (out-of-sight/out-of-mind). Further experiments are required to investigate if non-corvid food-caching species might be capable of truly cognitive tasks previously demonstrated only for corvids (e.g. episodic-like memory, recognition of specific individuals, etc.). Because environmental pressures are similar for many corvid and non-corvid food-caching species, it may be predicted that they may have evolved similar mechanisms in order to maximize cache recovery rates and to minimize cache theft. However, to demonstrate that chickadees might use corvid-like cognition, it is crucial to establish that chickadees can use observational memory, can recognize individuals and to show that caching decisions are affected by previous experience.

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