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Chickadees are selfish group members when it comes to food caching

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Abstract

Many food-caching animals live in groups and cache pilferage may be one of the negative consequences of social living. Several hypotheses have been proposed to suggest that individuals may benefit from caching even when cache pilferage is high if all individuals can cache and pilfer equally. Stable groups may hypothetically support the evolution of such “reciprocal pilfering” because all group members may potentially have numerous opportunities to pilfer each other’s caches. If that were the case, then we would expect animals cache openly in front of their group members, but to avoid caching in direct view of unknown conspecifics. We tested this hypothesis by allowing mountain chickadees (*Poecile gambeli*) to cache food in three experimental conditions: (1) with a familiar observer from the same group and with an unfamiliar conspecific observer present; (2) with a familiar observer from the same group only, and (3) without any observers. When presented with both a familiar and an unfamiliar observer, the caching chickadees treated both observers equally by choosing caching sites that were both farther away and out of sight of both observers. When only the familiar observer was present, chickadees shifted their choice of caching sites to the surfaces both away from and out of sight of the observer. When no observers were present, all available caching sites were used equally. Our results thus do not support the reciprocal cache sharing hypothesis and suggest that chickadees try to minimize cache pilferage from both familiar group members and unfamiliar conspecifics.

Keywords

cache pilferage; food caching; chickadee; cache pilferage prevention

Food-caching behavior appears to have evolved in response to changing and/or unpredictable environments in which survival may be strongly dependent on previously cached food (Vander Wall 1990). Food caching may be especially beneficial in social species because it may provide the individual with a competitive advantage during food shortage (Emery et al. 2004; Pravosudov 2008). To gain benefits from food caching, however, the caching individual should be able to recover its caches. Andersson and Krebs (1978) even argued that food caching should evolve only if the cachers have a higher probability of recovering their own caches than do other individuals. According to the Andersson and Krebs (1978) model, even a slight advantage at cache retrieval should be supported by natural selection.

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One of the main predictions from the Andersson and Krebs (1978) hypothesis is that food-caching species should evolve mechanisms allowing them to successfully retrieve their own caches. Indeed, there are numerous studies supporting this prediction. For example, most scatter-hoarding species are known to rely on spatial memory to recover their caches (Shettleworth 1995; Smulders et al. 2010). In addition, some scatter-hoarding species living in social groups use individual-specific physically non-overlapping sub-niches or foraging locations, which may also allow for successful cache recovery (Pravosudov 1986; Brodin 1994; Lens et al. 1994). Thus, it is clear that food-caching species do possess the means to recover their own caches.

A corollary of Andersson and Krebs' hypothesis is that food-caching species should also employ mechanisms that prevent cache pilferage (Emery and Clayton 2001; Pravosudov 2008). Maintaining an excellent memory for cached food would have no selective advantage if caches were always pilfered. Thus, there should be strong selection pressure for behavioral mechanisms that minimize cache pilferage. Most research on such pilferage-prevention behavior has been done with corvids, which appear to have evolved quite complex cognitive abilities allowing them to evaluate the risks of cache loss and to change their food-caching behavior accordingly (Emery & Clayton 2001; Bugnyar & Kortschal 2002, 2004; Bugnyar & Heinrich 2005; Emery et al. 2004; Dally et al. 2004, 2005a, b, 2006a, b). Corvids appear to 1) recognize specific individuals that observed them during caching events, 2) base their response to being observed on their own previous experience of stealing caches, 3) mislead their conspecifics when making caches, and 4) adjust their use of caching sites to prevent the transfer of visual information to potential cache pilferers (Emery & Clayton 2001; Bugnyar & Kortschal 2002, 2004; Bugnyar & Heinrich 2005; Emery et al. 2004; Dally et al. 2004, 2006a, b). Moreover, they appear to use observational memory to pilfer caches (Bednekoff and Balda 1996a, b). Thus, it is clear that corvids engage in cache protection strategies.

It has been suggested, however, that such complex cognitive abilities of food-caching corvids have evolved mainly because of their complex social environment rather than the demands of food caching and the risk of cache pilfering (Emery and Clayton 2004). One argument against food caching as the main impetus behind the evolution of complex cognition in corvids is that there is little evidence for similar cognitive abilities in other food-caching species such as parids (chickadees and tits; Emery and Clayton 2004, 2005). Parids live in social groups composed of unrelated individuals during the non-breeding season (Hogstad 1989; Harrap and Quinn 1995). Like corvids, many parids rely on cached food during the winter when food is scarce; consequently, successful cache retrieval (and thus the prevention of cache pilferage) should be important (Pravosudov & Lucas 2001). While parids undoubtedly use spatial memory for cache retrieval (Shettleworth 1995), laboratory studies have failed to show that memory use in parids is as long-term as in corvids (Hitchcock and Sherry 1990; Brodin and Kunz 1997). In addition, even though parids seem to be sensitive to cache pilferage (cache pilferage may affect choice of caching sites, Hampton and Sherry 1994), several studies have also failed to demonstrate that they pilfer caches using observational memory (memory of cache locations acquired by watching other individuals cache) (Baker et al. 1988; 1991; Hitchcock & Sherry 1995; Baker & Anderson 1995). Thus, there may be no need to conceal caching from conspecifics. Instead, it has been hypothesized that cache pilfering may be reciprocal and stable (Smulders 1998; see also Vander Wall and Jenkins 2003), whether by active pilferage (watching others cache and stealing those caches) or as a consequence of passive pilferage (finding caches by chance).

Pravosudov (2008), however, showed that chickadees do discriminate between potential pilferer and non-pilferer species and do adjust their caching behavior in the presence of

potential pilferers in order to minimize cache loss. Thus even though there is no evidence of observational memory use in parids, these birds do seem to engage in cache pilfer prevention. This study, however, did not address the issue of pilfer prevention among flock members. Instead, the logic of Smulders (1998) and Vander Wall and Jenkins (2003) suggests that reciprocity should be pronounced within stable social groups in which all individuals are familiar with each other, share the same territory during the non-breeding season, and thus have ample opportunities to reciprocate pilfering. In this situation, it would be expected that group members should share caches within the group but not outside of the group.

We tested this hypothesis using mountain chickadees (*Poecile gambeli*), which, like most other food-caching parids, form social groups during the non-breeding season (McCallum et al. 1999), by allowing these birds to cache in the presence of both familiar group members and unfamiliar conspecifics. We predicted that chickadees would cache in direct view of the familiar group member but would shift their caching to sites farther away and out of the direct view of unfamiliar individuals.

METHODS

We captured 22 mountain chickadees in September 2009 around Sagehen Creek, Tahoe National Forest, California. Birds were trapped at our network of 40 permanent feeders, which are spread over approximately 11 km along two forest roads (373 ± 37 m, mean $\pm$ SE between feeders). These feeders are spaced widely enough so that birds captured at different feeders belong to different social groups (Pravosudov, personal observations). To create the familiar groups, we selected one male and one female (sex based initially on wing length) that were caught in the mistnet simultaneously during a single visit by a single group of birds. In total, we formed 6 pairs to act as familiar group members and each pair was collected from separate flocks. We chose to use male-female pairs rather than same sex pairs to reduce aggression and the potential for competition. We also selected 8 single males captured at different locations from the known individuals to act as unfamiliar conspecifics.

After capture, all birds were transferred to the laboratory at the University of Nevada, Reno, and placed into wire-mesh cages. After 7 days in captivity, we collected 1 capillary tube (~ 75 μ l) of blood from the brachial vein of each bird to genetically verify sex as previously determined by wing chord measurement. DNA was extracted from samples using a Qiagen DNEasy kit (Qiagen Inc., Valencia, CA). Sex was determined by amplifying a portion of the sex-linked CHD genes (CHD-W in females only and CHD-Z in both sexes) in a polymerase chain reaction using microsatellite primers P2 and P8 (Griffiths et al., 1998).

Single males were housed individually in cages measuring $60 \times 42 \times 60$ cm. Male-female pairs were housed together in cages measuring $120 \times 42 \times 60$ cm. Pairs and single males were housed in two different rooms. Birds were initially housed on 11.5 h:12.5 h light/dark cycle, which was gradually decreased to 9.5 h:14.5 h light/dark by late October. Rooms were maintained at approximately 18°C. Birds were fed with unlimited amount of pine nuts, shelled and unshelled sunflower seeds, crushed peanuts, Roudybush bird pellets (Roudybush Inc., Woodland, CA) and with 6–10 mealworms daily. Water was provided *ad libitum*.

After a total of three weeks of adjustment to captivity, chickadees were familiarized with the experimental room ($218 \times 373 \times 263$ cm). The experimental room contained four caching “trees” made of dry pine trunks (ca. 10 cm in diameter) extending from the floor to the ceiling. These caching trees were positioned approximately 90 cm from the walls along the long side of the room and in the middle between the walls along the short side (Fig. 1). Trees were arranged in pairs in such a way that for each pair, the two sides facing each other

were at the same distance from the wall (Fig. 1). Each tree had 20 caching holes (6 mm in diameter, 5 mm deep), 10 on each of the two opposite sides either directly facing the observer or facing away (Fig. 1). The two lowest caching holes were about 40 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.

During familiarization, each bird spent three two-hour periods separated by two days in the experimental area. Pine nuts were available in two feeders as well as in some of the caching sites to stimulate caching behavior. As in our numerous other experiments in this system, all holding cages were connected to the experimental room by openings through the adjoining wall (e.g., Pravosudov & Clayton 2001 e.g., Pravosudov & Clayton 2002; Pravosudov 2008). This arrangement facilitated the movement of a subject, without handling, into and out of the testing room via the manipulation of lights (see Pravosudov & Clayton 2001 see Pravosudov & Clayton 2002, Pravosudov 2008).

After all birds were familiarized with the experimental setup, each individual chickadee from the paired birds was allowed to cache in the experimental room in three different conditions. In all experimental conditions, two cages ($25 \times 47 \times 31$ cm) were positioned at the two opposite sides of the room (along the long side; Fig. 1). Cages were positioned 47 cm above the floor. The front side of the cages was approximately 60 cm from the nearest caching tree; four caching surfaces (one on each tree) were oriented toward the cages (surfaces 1, 2, 7, 8) and the other four were on the opposite sides of the caching trees (surfaces 3, 4, 5, 6; Fig. 1A). In addition, surfaces 2 and 3 and surfaces 6 and 7 were at the same distance from the cages. Surfaces 2 and 7 were facing the cages; surfaces 3 and 6 were on the opposite sides (Fig. 1).

In the first experimental condition, one cage contained the other member of the pair (familiar observer) while the other cage contained one of the unfamiliar males (unfamiliar observer). In the second experimental condition, one cage contained the familiar observer while the other cage was empty. The third condition was a control treatment in which both cages were empty. In the first two conditions, the position of the familiar observer was determined randomly and then alternated between each trial to control for potential biases in room topography. For the analyses, the caching surface numbering always started from the closest surface directly facing the familiar observer (1) to the farthest (8 ; see Figure 1), thus the numbering was always relative to the position of the familiar observer. These three experimental treatments were systematically dispersed among the trials to avoid order effects.

All chickadees were tested individually for six trials (30 min each, 180 min total) during each of the three experimental conditions. During each trial, each bird was allowed to cache seeds in the experimental room. To stimulate caching, all birds were deprived of food two hours before the lights were turned off in the evening on a day before testing until testing the following day. Testing started one hour after lights were turned on in the morning. Five birds were tested each day and the order of birds tested was reversed between the trials to assure similar levels of food deprivation. Two feeders full of pine nuts were available at two opposite sides of the room. After birds were removed from the experimental room, the location of all caches was verified and recorded, 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; Pravosudov 2008). Experiments lasted from November 29, 2008 to April 4, 2009.

The diameter of the caching trees (ca. 10 cm) and the center location of each perch allowed the head and tail of the caching chickadee to extend slightly beyond the edge of the tree

(chickadee length is about 10–12 cm), providing a view of the observers. The caged observers were able to see the caching birds at all locations, but could not see the caching hole itself in any except the two sides of the first two trees closest to the observer. This arrangement simultaneously promoted the view of the observer(s) for the caching bird, but limited the caching views of the observers (Pravosudov 2008). Because trees were positioned directly in line between the two cages, the observers could only see the surfaces of the closest two trees directly facing them. In other words, observer 1 could see caching locations on surfaces 1 and 2, but not on any of the other caching surfaces, while observer 2 on the opposite side of the room could see only surfaces 7 and 8, but not the other surfaces. Our design also allowed discrimination between the effect of distance to the observer and the effect of the orientation of caching surfaces relative to the observers. Surfaces 2 and 3 and 6 and 7 were at the same distance from the respective observers, but surfaces 2 and 7 were directly facing the observers while surfaces 3 and 6 were hidden from the observers (Fig. 1).

For the statistical analyses, each bird contributed only one set of data. As we were interested in the distribution of caches made over all caching bouts, the total number of caches made by each individual on each available surface across all six trials (180 min) for each experimental condition was used as the datum. For each of the 6 trials, birds had unlimited amounts of food, 80 potential caching sites, and 30 min in which to cache. Consequently, over the course of the entire study, birds were likely not biologically limited by food and time available for caching as well as by caching sites available on 8 caching surfaces. To control for possible spatial biases in caching birds, the locations of the observers were alternated between each trial.

Because the caches made on the different caching surfaces by the same birds are not independent, a repeated-measures ANOVA was employed with surface as a repeated within-subject factor for each of the three treatments (two observers, one observer and no observers). In addition to analyzing all 8 caching surfaces (Fig. 1), we also collapsed surfaces 1 and 2, 3 and 4, 5 and 6, 7 and 8 into four combined surfaces. The resulting four surfaces (1 + 2; 3 + 4; 5 + 6; 7 + 8) allowed testing whether chickadees cache in direct view of the familiar observer, but avoid caching in direct view of an unfamiliar conspecific. If that were the case, we would expect no differences in the number of caches on surfaces 1 + 2, 3 + 4 and 5 + 6, but significantly fewer caches on surfaces 7 + 8. Alternatively, if chickadees avoid caching in direct view of any conspecific irrespective of whether it is a group member, we would expect fewer caches on combined surfaces 1 + 2 and 7 + 8 (in direct view by the observers) and more caches on combined surfaces 3 + 4 and 5 + 6 (hidden from both observers; Fig. 1).

Ethical note. All experimental procedures were in accordance with the University of Nevada Reno animal care protocol #00352.

RESULTS

When two observers were present, there were significant differences in the number of caches stored on different caching surfaces ($F_{7, 77} = 3.02$, $P = 0.007$; Fig 2A). When surfaces were collapsed into 4 categories depending on whether they were facing either of the observers or hidden from both observers (combined surfaces 1 + 2, 3 + 4, 5 + 6, and 7 + 8, Fig. 1), there were also significant differences in surface use ($F_{3, 33} = 4.83$, $P = 0.007$; Fig. 2B). Birds cached significantly fewer items on surfaces facing either of the observers (all P 's < 0.05) and more on surfaces facing away from both observers, i.e., the center-facing surfaces (Fig. 2B). There were no significant differences in the number of caches on surfaces facing either a familiar observer or an unfamiliar observer (all P 's > 0.3; Fig. 2B).

When only a single observer (the familiar observer) was present, birds again used available caching surfaces significantly differently ($F_{7, 77} = 3.29$, $P = 0.004$; Fig. 2C) from random. When 8 available surfaces were collapsed into 4 surfaces (1 + 2, 3 + 4, 5 + 6, and 7 + 8, Fig. 1), surface use remained significantly different from random ($F_{3, 33} = 5.51$, $P = 0.003$; Fig. 2D). Birds cached significantly fewer items in the trees closest to the observer (combined surfaces 1 + 2 and 3 + 4) while caching significantly more in the trees farthest from and out of direct view of the observer (combined surfaces 5 + 6 and 7 + 8; P 's < 0.04 ; Fig. 2D). Interestingly, combined surfaces 3 + 4 were not visible to the observer, yet chickadees used it significantly less as compared to the more distant and equally obscured combined surfaces 5 + 6 and 7 + 8 (Fig. 1, 2D). There were no significant differences between the number of caches on combined surfaces 1 + 2 and 3 + 4 ($P = 0.28$) or combined surfaces 5 + 6 and 7 + 8 ($P = 0.89$; Fig. 2D).

When no observers were present in the room, there were no significant differences in the use of caching surfaces, both when all 8 surfaces were analyzed ($F_{7, 77} = 0.73$, $P = 0.65$; Fig. 2E) and when the available surfaces were collapsed into 4 categories (1 + 2, 3 + 4, 5 + 6, 7 + 8; $F_{3, 33} = 0.92$, $P = 0.44$; Fig. 2F).

There was no significant difference in the amount of caching between treatments ($F_{2, 22} = 0.55$, $P = 0.58$, Fig. 3). There were also no significant differences in any of the measured parameters between males and females.

DISCUSSION

We failed to support the hypothesis that genetically unrelated, social food-caching chickadees potentially share caches with their group members by not concealing cache locations. We found that mountain chickadees attempted to conceal their caches from both familiar group members and unfamiliar conspecifics. When two observers were present, chickadees cached more items on the surfaces out of the observers' sight. When only the familiar group member was present, chickadees cached mostly on the surfaces farthest from and out of sight of the observer. When no observers were present, chickadees used all caching surfaces equally. Such results suggest that mountain chickadees are selfish cachers that attempt to minimize information about cache locations for all conspecifics, irrespective of familiarity and/or group identity.

These results are in line with the previous study showing that mountain chickadees avoid caching in direct view of potential cache pilferers (both conspecific and heterospecific) but ignore heterospecific non-pilferers (Pravosudov 2008). While Pravosudov (2008) argued that chickadees primarily used caching sites that could not be observed by potential pilferers, this study clearly indicates that chickadees also use distance as a potential way to reduce the risk of cache theft. Chickadees used caching surfaces both farthest from and least visible to the observers (Fig. 2).

When only one familiar observer was present, chickadees shifted their caching to the farthest caching surfaces instead of caching close to or in direct view of the group mate. Therefore, these data, together with the previous study (Pravosudov 2008), suggest that chickadees can employ at least two strategies, distance and out-of-view caching, both of which should reduce the risk of cache pilfering.

It is interesting to note that mountain chickadees did not reduce their caching rates in the presence of the observers, suggesting that their behavior was not likely a result of the perceived threat of immediate aggression by the observers. Available data suggest that parids are usually not successful at pilfering caches directly at the moment of caching (Lahti et al. 1998). Instead, cache pilferage seems to occur days or weeks after caching (Brodin

1993). The most important finding of this study, however, is that caching chickadees do not discriminate between their group members and members of other groups and they attempt to conceal their caches from all conspecifics.

Our results provide further support to the Andersson and Krebs (1978) hypothesis and suggest that chickadees have evolved behavioral mechanisms to reduce cache pilferage. Even though cache pilfer rates in chickadees may be high, cachers should still have an advantage at retrieving their own caches (Andersson and Krebs 1978). The fact that chickadees are aware of their social surroundings and change their food caching behavior to avoid caching in front of potential pilferers, including familiar group members, suggests that these birds are trying to prevent cache pilferage, which is consistent with the idea of individual cache use. It is unlikely that cache theft prevention tactics would have evolved if they were ineffective and if reciprocal cache pilferage were fully sufficient for the evolution of food caching as hypothesized by Smulders (1998) and Vander Wall and Jenkins (2003). Similar results were also observed in grey squirrels (*Sciurus carolinensis*), which treated all conspecifics as competitors (Leaver et al. 2007).

It is important to note that chickadee social groups consist of unrelated individuals. Thus, it remains possible that genetically related individuals, such as parents and their retained offspring, in some food-caching species (e.g., tufted titmice, *Baeolophus bicolor*; Siberian jays, *Perisoreus infaustus*, pygmy nuthatch, *Sitta pygmaea*, Harrap and Quinn, 1995) might indeed share food caches. In those species, parents may be investing in promoting the survival of their young, and food sharing may be one mechanism to enhance winter survival. Future research on species in which social groups contain genetically related group members are necessary to test this hypothesis.

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Figure 1.

Experimental room design. Numbers indicate all available caching surfaces. All numbering always started from the cage with the familiar observer, whose location was alternated between trials.

Figure 2.

Mean $\pm$ SE sum of caches made by mountain chickadees during 6 trials for each of the three experimental treatments on all 8 available caching surfaces (top panel, A, C, E) and on caching surfaces collapsed into 4 categories (1 + 2, 3 + 4, 5 + 6, 7 + 8) based on their orientation either towards or away from the observer (bottom panel, B, D, F). A and B – two observers present, familiar observer and an unfamiliar observer; C and D – only one known observer present; E and F – no observers present. Surface count always starts from the surface closest to the familiar observer.

Figure 3. Mean number of caches made by mountain chickadees during 6 trials for each of the three experimental treatments (two observers, one observer, no observers).