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Recaching Decisions of Florida Scrub-Jays are Sensitive to Ecological Conditions

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Abstract

Food caching animals depend on their caches at times of low food availability. Because stored food is susceptible to being stolen or degraded, many species employ cache protection strategies such as ceasing caching in the presence of others or avoiding storing perishable items for long periods. Several species frequently recover their caches and recache, which may reduce pilferage or degradation of cached items. We studied the food handling decisions of Florida scrub-jays (*Aphelocoma coerulescens*) after cache recovery to determine the roles that social and ecological environments play in post-recovery decisions. Instead of reducing recaching in the presence of others, recovering jays flew away from the recovery site, allowing them to eat or recache a recovered item regardless of the social context. Microhabitat type and soil moisture of the recovery sites had a significant influence on whether recoveries were eaten or recached; most items that were recached had been recovered from bare sand sites or sites with low soil moisture. Taken together, our results suggest that food store management of Florida scrub-jays are unaffected by the social context, but are strongly affected by the habitat conditions that influence the quality of caches.

Introduction

Decision-making involves trade-offs that can significantly influence fitness. One such trade-off for species living in habitats where food becomes seasonally scarce is whether to store food items for future but risk pilferage and degradation or to consume food immediately but risk not having enough food when conditions become harsh. Food storing (caching) has maximum benefits if cachers choose sites with low risk of pilferage and/or degradation (Vander Wall 1990). Many species regularly recover their caches (reviewed in De Kort et al. 2006), yet factors influencing the decision to eat or recache a food item after it has been recovered are not frequently addressed. In this study, we investigate the roles that social environment and habitat conditions play on food handling decisions after cache recovery in an endemic bird.

Food caching is common among several species of mammals and birds, including rats (McKenzie et al. 2005), squirrels, mice and chipmunks (reviewed in Vander Wall 2000), woodpeckers (Koenig & Mumme 1987), chickadees (Harrap & Quinn 1995), nuthatches (Woodrey 1990), tits (Lahti et al. 1998), and corvids (reviewed in Dally et al. 2006). When cached items are the critical food resource, the survival of caching individuals may depend on their food stores. For example, winter survival of acorn woodpeckers (*Melanerpes formicivorus*) is correlated with cache quantity (maximum number of acorns stored per bird) and quality (kJ stored per bird) (Koenig & Mumme 1987). However, because it has been estimated that individuals can lose up to a third of their caches each day to others (Vander Wall & Jenkins 2003; Dally et al. 2006), caching behavior would be adaptive only if individuals are more likely than conspecifics to recover their caches

(Andersson & Krebs 1978). Even heterospecifics may pilfer caches; for example, Steller's jays (*Cyanocitta stelleri*) steal caches of gray jays (*Perisoreus canadensis*, Burnell & Tomback 1985). Therefore, some species develop protection strategies such as reducing caching in the presence of others, defending cache sites, avoiding sites that have previously been pilfered (Dally et al. 2006), or moving caches around multiple times to reduce observers' spatial memory (Goodwin 1956).

Besides protecting their caches from pilferage, animals also need to avoid losing caches to environmental degradation. Humidity, temperature, and physical properties of the caching substrate all affect how quickly a cached item degrades (De Kort et al. 2006). Cached invertebrates are more susceptible to degradation than hard-shelled nuts and acorns (Clayton et al. 2006), but even nuts and acorns decay after long periods of storage under moist conditions. Western scrub-jays (*Aphelocoma californica*) cache both hard-shelled items and invertebrates and adjust their caching behavior by recovering perishable items before non-perishable items (Clayton et al. 2001). Squirrels preferentially cache acorns and seeds high in tannin (Smallwood & Peters 1986; Briggs & Vander Wall 2004) which is a phenolic compound that protects plants from insect predation and microbial decay (Fleck & Woolfenden 1997).

We suggest that decisions after cache recovery are influenced by trade-offs similar to those that pertain to caching decisions. Recaching allows animals to keep track of location and condition of their stores by reinforcing their memory (DeGange et al. 1989), minimizes pilferage if caches are moved to a new site, and protects against degradation (reviewed in Vander Wall & Jenkins 2003). However, cognitive demands for post-recovery decisions are different than initial caching decisions. First, animals must find their caches. Some species locate caches by olfactory cues under moist conditions but use their spatial memory in dry conditions, while others rely exclusively on spatial memory (Vander Wall 2000). Second, animals need to evaluate whether their cache is still viable. Third, animals may need to pay attention to their social environment during recovery (Emery & Clayton 2004). Therefore, post-recovery decisions are likely to be more complex, but equally important as the initial decision to eat or cache.

Florida scrub-jays (*Aphelocoma coerulescens*) provide a natural system to test the roles of ecological and social environment in post-recovery decisions because they frequently cache, recover, and recache acorns in the wild. Overall, jays allocate significant amount of time for recovery and recaching (DeGange et al. 1989). Acorns dry each time they are recovered (Bock 1970), and one possible motivation for frequent recovering and recaching may be to avoid fungal growth. Jays tend to eat acorns with low tannin content while caching those with high tannin (Fleck & Woolfenden 1997), and most caches are made just below the surface where moisture is lowest (Weekley et al. 2007), which might minimize degradation. Even though Florida scrub-jays are cooperative breeders living in groups composed of a breeding pair and helpers (usually offspring from previous seasons), cache pilferage occurs frequently when breeders pilfer from subordinates (DeGange et al. 1989; Kramer 2000). Therefore, caching decisions of subordinates are strongly influenced by the social environment (Toomey et al. 2007). In a closely related species, western scrub-jays, individuals with pilfering experience will protect their food items by recaching to a new place if they have been observed while caching (Emery & Clayton 2001). Because Florida scrub-jays live in groups, forage in the presence of others, and their initial caching behavior is influenced by the social context (Toomey et al. 2007), their frequent recaching behavior may also be influenced by the need to avoid pilferage.

Here, we test whether the decision to eat or recache a recovery is influenced by the social context or by the condition of the caches at the time of recovery. We expect that the decisions of dominant birds will not be influenced by the presence of conspecifics, but the presence of the breeding male or the breeding female will deter subordinate members from recaching a recovered item. We also expect that all jays will be sensitive to ecological factors, such as soil moisture of the recovery site, and will recache acorns recovered only from drier sites.

Methods

Study Site and Jay Caching Behavior

Our study site was Archbold Biological Station in south-central Florida in Highlands County. The jay population at the station has been studied since 1969 (Woolfenden & Fitzpatrick 1996), and all individuals were uniquely color-banded and habituated to human presence, allowing us to observe them without influencing their natural behavior. During our study period, the population had 65 breeding groups with a total of approx. 185 jays. Dominant vegetation at the site included xeric scrub oaks (*Quercus inopina,* *Q. geminata, Q. chapmanii,* and *Q. myrtifolia*), palmettos (*Serenoa repens, Sabal etonia*), and occasionally pines (*Pinus elliottii, P. clausa*).

Jays cache mostly acorns but may occasionally cache invertebrates and pieces of small vertebrates (I. G. Kulahci & R. Bowman, pers. obs.). Most caches are made in patches of bare sand with little or no vegetation, or under leaf litter or grass. Above-ground sites such as pine needle tufts, Spanish ball moss, and palmettos are used only for short-term storage. Each individual may harvest between 6500 and 8000 acorns during the late summer and fall, and caches are recovered during late winter or spring when insect abundance is at its annual nadir (DeGange et al. 1989). Caching activity consists of placing the acorn on the ground, hammering it below the surface, and finally covering the caching site with a leaf or twig. To recover a cache, jays insert their bill down vertically (plunge-probe), swipe across the cache site once or twice (sweep-probe), and then dig (excavation) (Bednekoff & Balda 1997). Immediately after recovery, jays assess the condition of the recovered item by manipulating it in their beak without breaking (DeGange et al. 1989, pers. obs.).

Data Collection

We observed post-recovery decisions through scan sampling at 5 min intervals during the breeding season between Mar. 15 and June 1, 2005. Observations were made during 7:00–11:00 and 14:00–18:00 with a total of 118 observation hours. We spent the first few minutes in each territory identifying jays to determine their age, sex, and social status (breeder vs. helper). When a jay started digging to recover a cache, we aborted the scans to begin data collection and continued observing the focal jay until the end of the recovery activities. We flag-marked the locations of recovery, recache, and eating sites and returned at the end of the day to these locations to measure the distances between them. We resumed scan sampling only after the recovery and caching activities of the focal jay ended. During the observations, the distance of other jays from the recovery site was estimated to the nearest meter. If multiple jays were present during recovery, we used only the distance of the closest jay in our analysis of whether the distance of others influences caching behavior. During rare cases in which recovering jays flew farther than 10 m, we followed them after placing a flag on the recovery site. If we lost sight of a jay after recovery because of dense vegetation, the recovery was excluded from our analysis. Only once did two jays make simultaneous recoveries, however, both remained in sight until they ate their acorns.

Soil moisture is lowest in the top 10 cm of the soil (Weekley et al. 2007), and jays preferentially cache within the top few centimeters of the soil (I. G. Kulahci & R. Bowman, pers. obs.). We recorded the moisture at recovery and recache sites with a Kelway Model HB-2 soil moisture meter (Kel Instruments Co. Inc., Wyckoff, NJ, USA). Our moisture probe was most accurate if its tip was completely immersed in the soil, and we taken our measurements within the top 10 cm of the soil. All the readings were taken from undisturbed soil within 1cm of the recache or recovery sites. We did not obtain moisture of above-ground sites such as twigs, small holes in trees, moss, or palmetto fibers.

Data Analysis

We analyzed social factors such as age, sex, dominance status of the recovering jay (available through the census records at the Archbold Biological Station), the number of other jays present, dominance status of present jays and their distance from recovery site. Ecological factors included date, recovery and recache site microhabitat (sand, leaf litter, grass, and above-ground), and moisture. We log-transformed soil moisture data and square root transformed distance flown after recovery data. We entered all of social factors and their interactions into a logistic regression fit model to analyze the effects of the social factors on the decision to eat or recache a recovery. We repeated the same analysis for the ecological factors. Non-significant interactions were removed from the final models. We used ANOVA to test which factors, including number of jays present at the recovery site and their status, and the status and the age of the focal jay, influence how far the focal jay flew before recaching or eating a recovered item. The potential effects of date and the microhabitat type on soil moisture levels were analyzed using ANOVA followed by *post hoc* Tukey test. Differences between moisture of recovery site and the subsequent recache sites were analyzed with a paired-samples t-test. All analyses were carried out in JMP Statistical Software (JMP v.7; SAS Institute Inc., Cary, NC, USA).

Results

Decision to Eat or to Recache

We recorded a total of 102 recoveries, but excluded five of these recoveries from our analysis because we were not able to reliably observe whether the recovered items were eaten or recached. Of the remaining 97 recoveries by 71 jays, 24 were recached, 68 were eaten, and five were discarded. Of these 71 jays, 19 jays (%27) recovered their caches twice, while 52 jays (73%) made a recovery only once. Only one jay recached twice, while 22 jays (32%) recached once and the remaining 48 jays (67%) did not recache their recoveries. The decision to eat or recache the recovered item was not influenced by the social status (Logistic fit; breeder vs. helper, $\chi^2_6 = 3.404$, $p = 0.757$, $n = 51$, 46 individuals, respectively), age ($\chi^2_{14} = 12.588$, $p = 0.559$, $n = 70$), sex ($\chi^2_1 = 1.204$, $p = 0.548$, female recoveries = 41, male recoveries = 56), or identity ($\chi^2_{70} = 113.38$, $p = 0.938$, $n = 95$) of the recovering jay, nor by the number of jays present at the time of recovery ($\chi^2_8 = 8.048$, $p = 0.428$), their social status ($\chi^2_4 = 2.454$, $p = 0.653$) or their distance from the recovery site ($\chi^2_2 = 0.208$, $p = 0.546$). Females were never observed recovering alone; all of their recoveries were during times when they were together with either the breeding male of the group (n = 27) or a helper male (n = 14).

All of the items recovered during this study were acorns. Recaching activities of the jays decreased as our study progressed from Mar. to June, and lower ratios of recovered acorns were recached later in our study (Logistic fit: $\chi^2_2 = 9.503$, $p = 0.009$, $n = 97$) (Fig. 1). Majority of the recached acorns had been recovered from sand sites instead of leaf litter and grass sites ($\chi^2_2 = 10.081$, $p = 0.006$; n = 32, 39, 20 for sand, leaf litter, grass recoveries; Fig. 2). Overall, an acorn was recached only if it had been recovered from a low moisture site (≤15% moisture), and greater ratios of recovered acorns were eaten instead of recached as the soil moisture increased ($\chi^2_2 = 9.641$, $p = 0.081$) (Fig. 3). The choice of the recovery site was not influenced by the identity of the jays (Logistic fit: $\chi^2_2 = 184.87$, $p = 0.863$, $n = 95$).

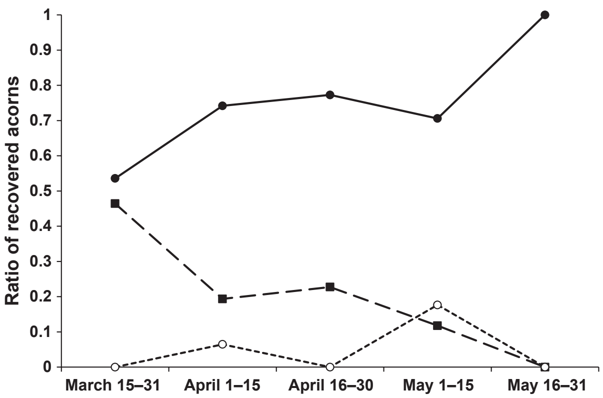

Fig. 1: Seasonal variation in the ratio of recovered acorns (N = 97) that were eaten (n = 68, gray), recached (n = 24, black), or discarded (n = 5, white/dashed). Later in season, more recoveries were eaten (n = 14, 38, 16; for Mar., April, May) than recached (n = 12, 10, 2). Acorns were discarded only in April and May (n = 2, 3).

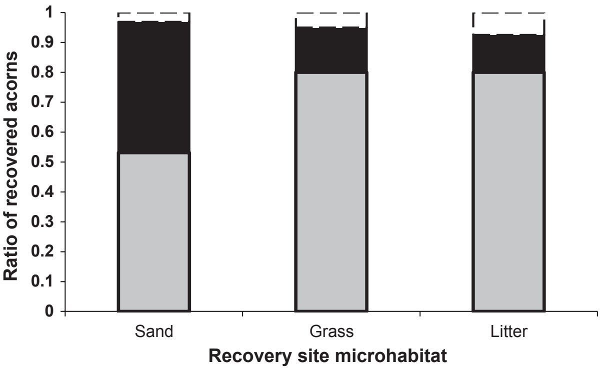

Fig. 2: The ratio of recovered acorns that were eaten (gray), recached (black), and discarded (white/dashed line) varied by microhabitat. A higher proportion of caches from sand (14 of 32 recoveries) were recached relative to leaf litter (five of 39 recoveries) and grass sites (three of 20 recoveries).

Moisture of the Recovery Site

Soil got dryer as the season progressed (ANOVA: $F_{1,87} = 5.758$, $p = 0.019$). The microhabitat type also influenced the moisture levels ($F_{2,87} = 5.463$, $p = 0.006$); a *post hoc* Tukey revealed that the sand sites

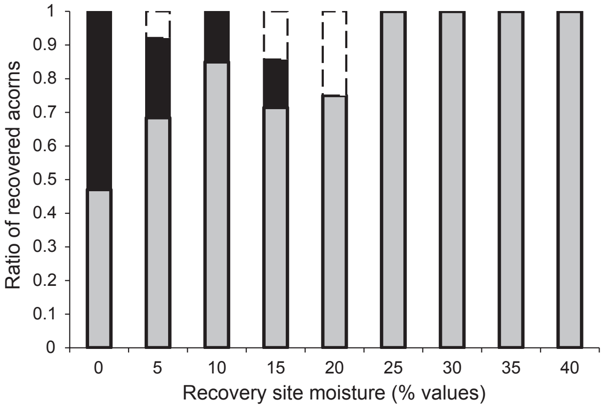

Fig. 3: Variation in ratio of recovered acorns that were eaten (gray), recached (black), or discarded (white/dashed) from recovery sites with different levels of soil moistures (all microhabitats combined). More acorns recovered from lower moisture sites were recached than high moisture sites, and all acorns from sites with moisture ≥25% were eaten (number of recoveries = 17, 38, 20, 7, 4, 2, 1, 2, 1 for moisture levels in 5% increments from 0 to 40%).

had lower moisture (mean ± SD = 5.937 ± 2.278% moisture, n = 32) than leaf-litter (9.230 ± 3.314, n = 39), but moisture of grass sites were not significantly different than leaf litter or sand because of high levels of variation (9 ± 7.88, n = 20). The above-ground sites (n = 6) were excluded from the moisture analysis. Moisture of the recovery sites (8.03 ± 7.6, n = 91) was not significantly different than the moisture of the corresponding recache sites (6.25 ± 4.72, n = 21), (Paired samples t-test: t = 1.092, df = 20, p = 0.287).

Distance Flown After Recovery

Overall, jays flew longer distances before recaching (mean ± SD = 4.110 ± 0.342 m, n = 24) than before eating an item (3.154 ± 0.206, n = 66) (ANOVA: $F_{1,89} = 5.574$, p = 0.018). However, if the recovery was made when a jay was alone, then there was no difference in the distance flown before eating or recaching ($F_{1,23} = 0.492$, p = 0.491). Jays made the decision to discard a recovered item at the recovery site (I. G. Kulahci & R. Bowman, pers. obs.); therefore, the discarded items were excluded from the distance analysis. The number of jays present at the recovery site was positively correlated with the distance flown from the recovery site (Fig. 4, ANOVA: $F_{4,82} = 6.335$, p = 0.0002); jays flew shortest distances when alone (2.75 ± 0.30, n = 25) and longest distances when in the presence of four jays (5.88 ± 0.58 m, n = 7). *Post hoc* Tukey comparison revealed that distance flown in the presence of one, two, or three jays were not different from each other, but all were significantly shorter than distance flown in the presence of four jays and significantly longer than distance flown when jays were alone (3.232 ± 1.48; 3.342 ± 1.88; 4.205 ± 2.08 m; n = 39, 15, 9 for 1, 2, 3 jays). Neither the social status ($F_{3,82} = 0.066$, p = 0.978) nor the age ($F_{7,82} = 0.994$ p = 0.443) of the recovering jays influenced how far they flew.

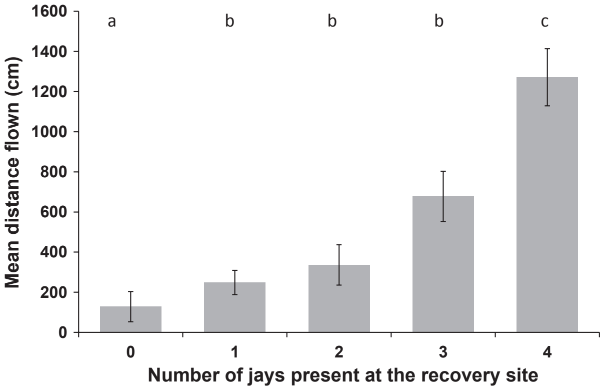

Fig. 4: The number of jays at the recovery site was positively correlated with the distance that recovering jays flew before eating or recaching. Different letters indicate significant differences. Jays flew shortest distances when they were alone (n = 25) and longest when in the presence of four jays (n = 7). The distances flown in the presence of one, two, or three jays (n = 39, 15, 9, respectively) were not different from each other.

Discussion

The decision of Florida scrub-jays to eat or recache their recoveries was independent of their own and nearby jays' social status, age, and sex. Even though social environment did not influence the post-recovery decision, the distance flown by jays after recovery was positively correlated with the number of jays present at the recovery site. Jays ate a higher proportion of recoveries from bare sand patches, from sites with low soil moisture, and later in the season. Soil moisture changed seasonally but was mostly influenced by microhabitat type, because bare sand patches were drier than leaf litter sites. Together, our results suggest that the food-handling decisions of Florida scrub-jays after cache recovery are unaffected by the social context, but are strongly affected by the habitat conditions that influence the quality of caches.

Microhabitat and soil moisture influence the post-recovery decisions possibly by affecting condition of caches. Florida scrub is composed of different vegetative associations that vary in their soil moisture content (Weekley et al. 2007), and our results show that within those associations, moisture can differ among microhabitats such as bare sand, leaf litter, or grass. Sand sites may be better caching substrates than leaf litter or grass sites due to their low moisture content, which would minimize degradation. Florida scrub-jays, similar to Mexican jays (*Aphelocoma ultramarina*) (Hubbard & McPherson 1997), can evaluate cache condition by manipulating acorns in their beak without opening them (DeGange et al. 1989), and thus may recache only the acorns in good condition.

Caching decisions of other species, such as grey squirrels (Hadj-Chikh et al. 1996) and Western scrub-jays (Clayton et al. 2005) are also sensitive to the condition of their caches. For example, Western scrub-jays cache different types of items such as nuts and mealworms, and if they encounter a degraded item (such as a mealworm), they reduce caching similar items in subsequent caches (Clayton et al.

2005). If Florida scrub-jays respond to degradation in a similar way, we would expect them not to recache items which have been stored for longer periods. Even though we do not know when the acorns in our study were originally cached, acorns that were recovered later during our study had most likely been buried for longer periods than acorns that were recovered earlier, because most fresh acorns are harvested and cached before late winter (DeGange et al. 1989). Consistent with our expectations, jays recached lower proportion of their recoveries later in the season. It is also possible that lower caching rates observed later in the season were because of a change in food availability (reviewed in Pravosudov 2006), as jays may have started running out of stored food items in May when they made fewer recoveries than April (n = 22 and 53, respectively).

Many studies, including a study on the same population (Toomey et al. 2007), have shown that subordinate individuals avoid caching in the presence of others (reviewed in Dally et al. 2006). The influence of social context on caching behavior is observed in several taxa and has led to the suggestion that caching and pilfering strategies may have co-evolved in an arms race (reviewed in Grodzinski & Clayton 2010). We had expected that the decision to eat or cache after cache recovery would also be influenced by the social context. However, contrary to our expectations, presence of others during recovery did not lead to lower recaching rates. We also found no significant influence of identity, age, sex, and status on post-recovery decisions. It is possible that our results were influenced by factors that we did not have any control over, such as whether areas around recovery sites had been pilfered before, because birds avoid caching in previously pilfered sites (Kamil et al.1993; Hampton & Sherry 1994), or whether recovering jays were experienced pilferers (Emery & Clayton 2001) and were pilfering instead of recovering their own caches. We suggest two reasons may have influenced why jays did not reduce caching in the presence of others in our study.

First, since many birds use observational spatial memory to pilfer caches (Clayton et al. 2007), flying farther from conspecifics, instead of reducing caching, may have been used as an alternative strategy to reduce pilferage. Our study differs from some of the previous studies because jays in our study recovered and recached in their natural environment, instead of in situations which offer limited caching space or provide resources concentrated in one place (Lahti et al. 1998) or time (Toomey et al. 2007). Similar to jays, chickadees also do not reduce caching rates when they have the option to cache at a distant site (Pravosudov 2008). Other species also employ similar strategies including flying further from food source in the presence of others (gray jays (*P. canadensis*), Waite 1992; Black-capped chickadees (*P. atricapillus*), Baker & Anderson 1995; willow tits (*P. montanus*), Lahti et al. 1998), caching out of view (common ravens (*Corvus corax*), Bugnyar & Kotrschal 2002; Western scrub-jays, Dally et al. 2006), caching in hard-to-see sites (common magpie (*Pica pica*), Clarkson et al. 1986; Western scrub-jays, Dally et al. 2004), or increasing spacing between caches (grey squirrels (*Sciurus carolinensis*), Leaver et al. 2007).

Second, most caching studies have been based on decisions during initial caching rather than decisions after recovery. To our knowledge, post-recovery decisions have been investigated only in one study (Clayton et al. 2007) that addressed whether being observed at the time of initial caching led to higher rates of recaching later. However, addressing the influence of social context during recovery was not a part of this study, because jays recovered their caches in private. Therefore, it is possible that post-recovery caching decisions present a unique situation that requires different strategies. Yet, this behavior currently remains under-studied.

As most jays recovered only once during our study, and only one jay recached more than once, we do not have replicate measures from majority of the jays. Therefore, we were not able to address whether individual variation, such as differences in boldness levels (Sih et al. 2004), influenced jays' decisions after cache recovery. In group living species like Florida scrub-jays, bolder individuals may be more likely to forage alone instead of among group members, which may influence their decisions such as choice of recaching sites or distance flown after recovery. While it is possible that individual variation among jays has a major influence on decisions, our data does not allow us to address this possibility. Therefore, future long-term studies that analyze individual variation by recording repeated recoveries and recaches from same individuals would be very valuable for determining the robustness of the effects of environmental factors and for addressing whether individuals vary in how they respond to the environmental factors that may influence post-recovery decisions.

We suggest that in future studies, analyzing conditions during recovery and recaching will provide valuable insights into the cognitive demands of caching and the challenges faced by species that manage their food stores over long periods. Ideally, such studies should also keep track of individual differences. In our study, Florida scrub-jays responded to the social context during cache recovery by flying farther when many jays were present, but their decision to eat or to recache was correlated only with the ecological factors which influence the viability of caches. Our results, when viewed together with other studies, point toward a possible trend that deserves more exploration; if caching species are given the opportunity to change their social environment by avoiding locations around conspecifics, their long-term food management decisions may depend mainly on the perishability of their caches.

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